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BOREAL FOREST REGENERATION DYNAMICS: MODELING EARLY FOREST ESTABLISHMENT PATTERNS IN INTERIOR ALASKA

A

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By

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BOREAL FOREST REGENERATION DYNAMICS:
MODELING EARLY FOREST ESTABLISHMENT PATTERNS IN INTERIOR ALASKA

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ABSTRACT

Ecological processes are responsible for vegetation trajectory within the boreal forest landscape of interior Alaska. The reproductive response of boreal forest to disturbance controls vegetation trajectory. Boreal forest reproduction dynamics are influenced by both biotic and abiotic factors, acting upon the spatio-temporal dynamics of the landscape. Understanding these factors and how the boreal forest responds, both spatially and temporally, is critical for the development of accurate models of regional and global vegetation dynamics. I developed a geographic model of the early post-disturbance seedling regeneration pattern of upland white spruce ecosystems in interior Alaska. The model was developed and runs within a geographic information system (GIS). The model simulates the establishment patterns of white spruce, paper birch, and aspen across the landscape following fire. Seed production and dispersal, disturbance effects upon the seedbed, and the early establishment of both seedlings and vegetative stems are simulated. The model was used to simulate a 6 yr period (1983-1988) of seedling establishment at the Bonanza Creek Experimental Forest near Fairbanks, following the Rosie Creek fire. Correlation values between predicted and established seedlings were high, demonstrating the model's ability to simulate general establishment patterns. Sensitivity analysis revealed seed production, seed source location and orientation, and seedbed "receptivity" as important controls upon the early establishment success of white spruce seedlings following disturbance. Establishment patterns between a hypothetical clearcut, strip-cut, and residual tree islands cut were simulated and compared. Distance from the seed source was identified as a major limitation to adequate stocking levels in the clearcut. The residual islands cut provided the highest stocking levels, followed by the strip-cut and clearcut. The results suggest large clearcuts are not an efficient harvesting method in interior Alaska for successful natural regeneration and stocking levels. The model results warrant further development and identified a "real" potential use as a forest management tool.

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CHAPTER 1 - INTRODUCTION

Societal demand for both forest products and conservation of forested ecosystems has created the need for a sustainable forest management program. A solid understanding of post-disturbance early regeneration dynamics is imperative to successful sustainable forest management. This study describes a geographically explicit model of early post-disturbance seedling establishment patterns for upland white spruce ecosystems in interior Alaska. Key factors and processes important in post-fire establishment patterns are examined. This study provides an increased understanding of post-fire regeneration dynamics and provides a management tool for analysis of the reproductive potential of a disturbed site.

The Landscape Mosaic

Terrestrial landscapes are composed of a mosaic of heterogeneous land forms, vegetation types, and land uses (Urban et al. 1987). The driving variables of landscape pattern formation include disturbance, biotic processes, and environmental factors (Levin 1978). This mosaic pattern reflects the disturbance history of the area and its interaction with ecological state factor controls. The state factors of time, topography, regional climate, the biota, and parent material function independently of the ecosystem and determine ecosystem development (Jenny 1980). The state factors condition the ecosystem controls that directly affect system structure and function. These controls change through time as ecosystem development occurs (Van Cleve et al. 1991). Major

(1951) elucidated this state-factor approach, applying it to vegetation properties. It is this heterogeneous property, both spatially and temporally, of ecosystem controls that result in the vegetation mosaic characteristic of interior Alaskan boreal forest.

The Alaskan boreal forest is driven by a cold-dominated environment that is regionally modified by topography causing dramatic consequences in ecosystem structure and function. Furthermore, ecosystem development is conditioned by disturbance, principally fire in the uplands and fluvial processes on the floodplains (Van Cleve et al. 1991, 1996). It is from this state-factor approach that studies of ecosystem processes in Alaska have been carried out (Crocker and Major 1955, Heilman 1966, Viereck 1970, Van Cleve et al. 1991, 1996).

Computer Models and Forest Succession

Computer models of forest succession have identified processes important in ecosystem development. Several mathematical modeling approaches have been developed to investigate forest succession and successional processes. Models of succession can be divided into three basic categories: individual tree, gap or stand, and landscape models. Furthermore, within any category there are both spatially and nonspatially referenced models.

Models of individual trees simulate growth of an individual plant. These models simulate complex processes of carbon and nutrient allocation, photosynthesis, respiration, and evapotranspiration (Huston 1991). An example of such a model is ECOPHYS (Rauscher et al. 1991). Other individual tree models simulate probability of

replacement, such as Horn's (1975a, b) Markovian replacement probability prediction model. Others include competitive response of individual canopies. Another example of an individual tree based model of succession is FOREST (Ek and Monserud 1974). Many of these models describe physiological processes and conditions that are used in other modeling approaches.

Gap models are a subcategory of individual tree models. Gap models simulate succession by calculating the competitive interrelations among individual trees in a restricted spatial unit - either a gap created by the death and removal of a canopy tree or a sample quadrat (Shugart and West 1980). These models emphasize plant competition for light and resources, the most well known being JABOWA (Botkin et al. 1972a, b) and FORET (Shugart and West 1977). Gap models operate with timesteps of months to a year and at a spatial scale of 0.1 to several hectares. Urban et al. (1991) describe the application of a gap model to simulate forest patterns at landscape and geographic scales.

Landscape models work at the scale of many hectares to square kilometers. These models incorporate ecosystem processes such as seed dispersal, fire spread, and patch dynamics. The models generally do not explicitly simulate processes at the individual or gap-level, but rather implicitly represent such processes through more generalized response functions. These models characterize vegetation patterns across the landscape, large scale ecosystem processes, or issues such as climate-vegetation-atmosphere interactions (Huston 1991). FIRE-BGC (Keane et al. 1996) is a landscape

model that simulates the long-term stand dynamics of forest landscapes in the Rocky Mountains. The model deals with ecosystem processes such as seed dispersal, tree growth, and decomposition. It is a coupling of two different ecosystem models; the gap-replacement model FIRESUM (Keane et al. 1989) and a biogeochemical simulation model FOREST-BGC (Running and Coughlan 1988, Running and Gower 1991).

Modeling Forest Establishment Patterns

Two recent examples of spatially explicit models highlight application of models for forest establishment simulations. The REGROW model (Mou and Fahey 1993) simulates early recolonization of hardwood species following clearcutting of a northern hardwood forest in New Hampshire. The spatial component of the model allowed for investigation of factors affecting recolonization patterns and interactions between individual seedlings for resource acquisition. The model allows investigation of the effects of initial density, composition and spatial patterns of seedlings upon establishment patterns. Busing (1995) used the spatially explicit model STORM (Busing 1991) to investigate regeneration dynamics of yellow popular (Liriodendron tulipifera) in Appalachian cove forests during forest development. The spatial component of the model identified a crucial gap size associated with yellow popular recruitment. Model results identified disturbance during forest development was an important control on establishment of yellow popular natural regeneration.

Kellomaki et al. (1987) and Pukkala and Kolstrom (1992) used spatially explicit models to investigate natural regeneration in Scots pine (Pinus sylvestris). The studies modeled seed crops, seed dispersal, germination, survival and establishment, and growth of seedlings. The models illustrate the effect of density and spatial distribution of the parent trees and the resultant influence upon seed dispersal and seedling survival and growth. Pukkala and Kolstrom (1991) also modeled the effects of Norway spruce (Picea abies) spatial patterns on stand development.

There has also been significant modeling work based upon the traditional gap-model, JABOWA. Kellomaki and Kolstrom (1992) investigated species composition and organic matter accumulation in Finland in relation to changing climate, using the JABOWA model. Successional processes related to carbon and nitrogen dynamics, indicated a potential shift in species composition in response to an increase in temperature. Bonan (1988, 1989a, b, 1991, 1993) and Bonan and Korzuhin (1989) have used a gap-based model to investigate and simulate various environmental factors and ecological processes critical in driving vegetation patterns in upland boreal forests of North America, with particular regards to ecosystem structure and function in interior Alaska.

There are two fundamental shortcomings exhibited by the majority of models discussed above. The first involves the regeneration component represented by a simplified reproduction process, particularly within the gap models. This over-simplification creates an unrealistic picture of the regeneration process and simulates

only general vegetation patterns and succession. For example, gap models assume availability of a seed source and associated seed (Botkin et al. 1972a). Issues of seed source availability and irregular seed production are not addressed and yet are important to the natural regeneration process and vegetation patterns of the Alaskan boreal forest (Zasada et al. 1983, 1992, Zasada 1986, 1995). Bonan's (1988) gap model of boreal forest vegetation patterns does not simulate irregular seed production or the effects of disturbance upon seed source availability. The present study investigates the importance of this early regeneration process upon vegetation patterns, specifically dealing with issues of irregular seed production, seed source availability, and effective dispersal distance.

The second fundamental shortcoming is that most forest succession models are not spatially explicit. Spatially explicit models are models whose dynamics are represented on a discrete landscape, represented as a grid of cells (Mou and Fahey 1993). Such representation allows for explicit coordinate location of interacting individuals and resources. This in turn allows for simulation of spatial interactions, horizontally and/or vertically, related to forest succession and successional processes. However, this spatial representation is not geographically referenced and therefore does not represent a geographically defined landscape unit. Inferences can be made from the model results, but must be regarded within the context of the model framework. In other words, potential application to a "real-world" landscape is dependent upon the similarity of the "model" landscape and that of the "real-world"

landscape (i.e. topography, climate, parent material, etc.). A geographic information system (GIS) provides the framework for the "model" and "real-world" landscape to be the same.

A geographic approach to modeling provides for a geographically defined landscape and the ability to model at various spatial scales. For the most part, the use of GIS in forest ecosystem modeling has been in the presentation of results, derived from some other simulation code (i.e. FORTRAN). Some models such as DISPATCH (Baker et al. 1991) and FIRE-BGC (Keane et al. 1996) utilize a GIS for managing spatial data and presentation of results. However, few models have been developed that function entirely within a GIS framework. The models GAFED by Yarie (1997) and ABFEM (Alaskan Boreal Forest Establishment Model), presented here, are the only two GIS-based models of interior Alaskan forest development and successional processes. This study presents the geographically referenced model ABFEM. This relatively unique modeling approach will be described and both advantages and disadvantages of the approach will be discussed. Furthermore, controls upon post-disturbance establishment and vegetation patterns for interior Alaskan forest ecosystems at the landscape-level will be presented.

Study Objectives and Hypotheses

The objectives of this research are three-fold. First, to develop a model entirely in the framework of a GIS. Second, to model early post-disturbance establishment patterns of interior Alaska white spruce ecosystems. Third, to identify important

environmental factors and ecological processes that influence early establishment and vegetation patterns.

The following testable hypotheses follow from the research objectives:

1. Establishment patterns of interior Alaska white spruce forests are strongly influenced by seed production and dispersal and the post-disturbance characteristics of the seedbed. For example, a spatial model of white spruce seedling establishment would be dependent on the location of seed sources, and the production and dispersal of viable seed on a site recently disturbed; the success level of natural regeneration will be controlled by both seed production level and vegetative competition for growing space.

2. White spruce seed rain pattern and density are influenced by the extent and orientation of the seed source, irregular cone production, topography, and wind. These factors are interrelated and given a specific set of circumstances, directly affect landscape-level natural regeneration patterns, both temporally and spatially.

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CHAPTER 2 - CONTROLS UPON FOREST ESTABLISHMENT PATTERNS

The developmental history of a forest ecosystem can provide information concerning patterns and mechanisms of establishment. The disturbance regime, plant reproductive strategies, and successional pathways interact to drive forest establishment. Controls over establishment, specific environmental factors and ecological processes and their interactions, directly influence these patterns and mechanisms. This chapter reviews the developmental history, environmental factors, and ecological processes important to the establishment patterns of interior Alaska forest ecosystems. Furthermore, I develop a simple conceptual view of early establishment (Figure 2-1), identifying the key factors and processes represented by the model, which drive the simulated establishment and vegetation patterns.

Developmental History

Disturbance Regime

A disturbance is a discrete, punctuated killing, displacement, or damaging of one or more individuals that directly or indirectly creates an opportunity for new individuals to become established (Sousa 1984). Natural disturbance, including fire, flooding, windthrow, and insects and disease, plays a central role in determining the course of ecosystem development. The boreal forest of interior Alaska is dominated by a mosaic of young stands in various stages of succession (Van Cleve and Viereck

1981). This mosaic pattern is the direct result of the natural disturbance regime of the boreal forest.

Floodplain systems are dominated by fluvial processes of erosion, inundation, and sedimentation. These fluvial processes drive both primary and secondary successional pathways. Mann et al. (1995) found evidence of frequent fires within the backswamp and meander belt areas of the Tanana River floodplain that are characterized by older terraces and the occurrence of black spruce, suggesting fire also plays a key role in floodplain secondary succession, also noted by Van Cleve and Viereck (1981).

In the uplands, fire is the main disturbance that resets the successional clock (Van Cleve et al. 1991). Its frequency and severity are major influences on the vegetation structure, composition, productivity, and virtually all ecosystem processes (Yarie 1981). Yarie (1981) calculated fire cycles on the order of 50-100 years for interior Alaska forests. Lutz (1956) completed an exhaustive study of the ecological effects of fire in interior Alaska. Several significant reviews of wildfire in the boreal forest, both in Alaska and Canada, have followed (Viereck 1973, Kelsall et al. 1977, Viereck and Schandelmeier 1980). Most interior Alaska forest fires are relatively high intensity crown fires or severe surface fires that kill and regenerate entire stands (Heinselman 1981).

The relative importance of windthrow, insects and disease within the disturbance regime of the Alaska boreal forest and its affects upon landscape-level

vegetation patterns and successional pathways are unclear. Windthrow at the landscape-level, as large-scale blowdown events, is not part of the general disturbance regime of interior Alaska. Insect outbreaks, particularly the spruce beetle (Dendroctonus rufipennis) and spruce budworm (Choristoneura fumiferana), have recently contributed significantly to the disturbance regime at both the stand- and landscape-level (Werner and Holsten 1983, Holsten 1990, Werner 1994, 1996, Burnside et al. 1995).

Other disturbance agents, such as snow breakage and animal browsing affect the structure and function of the boreal forest landscape. Van Cleve and Zasada (1970) documented the effects of snow breakage on stands of white and black spruce in interior Alaska. During the winter of 1967-1968 twenty-three percent of the stems within a 178-year-old white spruce stand were broken, resulting in the deposition of 13.3 metric tons per hectare of white spruce crown and stem material. Sampson and Wurtz (1994) reported significant snow breakage in stands of white spruce and aspen-birch during the winter of 1990-1991. These events many times involve either early heavy snows or a combination of rain and snow. Time of occurrence appears to be an important factor for snow breakage events, which can cause significant changes to stand structure.

Herbivore browsing can have a significant impact on the vegetation and influence successional pathways, shifting community structure toward unbrowsed species (Pastor and Naiman 1992). Bryant (1987) found evidence to suggest heavy

browsing by snowshoe hare may be an important control over primary succession on floodplains in Alaska. The reduction in height of willow by hare browsing may result in shading of willow by alder. Molvar et al. (1993) found that moose browsing of diamondleaf willow caused significant vegetation growth in treeline plant communities in central Alaska. Increased moose densities affect nutrient cycling rates, indicating moose may mediate rates of nutrient cycling in northern ecosystems (Kielland et al. 1997).

Fire, the principle disturbance agent of the Alaska boreal forest, is closely tied to other agents of disturbance. Fire occurs at a long-term return interval, relative to other disturbance agents. For instance, snow breakage or insect attack may occur several times between fires. The timing of certain events, such as insect outbreaks, is influenced by fire, and fire is subsequently affected by the timing and severity of these disturbance events. These disturbance events increase tree mortality and subsequent fuel loads that increase the flammability of affected systems. For example, insect outbreak and fire have historically been closely linked. Insect outbreak causes mortality and increased fuel loads, which increases the probability of fire. Fire episodically acts as a cleansing factor, destroying insect populations and removing insect host sites (Heinselman 1981, Ahlgren 1974, Richardson and Holliday 1982, Sherman and Warren 1988). Trees injured or killed by fire also can attract insects, Evans (1971) listed several insect species attracted to forest fires.

The general disturbance regime of the Alaska boreal forest plays a critical role in forest establishment patterns. The interaction between disturbance, especially fire, and the boreal forest is evident in the reproductive strategies and successional pathways of these northern forests.

Reproductive Strategy

Plants utilize various strategies or modes of reproduction to become established, increase post-establishment abundance, and survive disturbance and environmental change (Wagner and Zasada 1991). Grime (1979) describes in detail the various strategies employed by plants. Cattelino et al. (1979) utilize plant strategies to model successional pathways following disturbance. The reproductive strategies exhibited by species generally reflect specific effects of the disturbance regime characteristic of the ecosystem. This is particularly evident with regards to tree species of interior Alaska, for example the semiserotinous cones of black spruce or the suckering strategy of aspen..

Tree species of the Alaska boreal forest use several different strategies of reproduction following disturbance. Species have evolved particular strategies that best exploit their regeneration niche, as defined by Grubb (1977). These strategies can be categorized into either sexual or vegetative reproduction. Sexual reproduction involves the production and availability of reproductive buds and the subsequent

production of a seed crop. Vegetative reproduction involves both clone expansion and regrowth from the bud bank (Zasada et al. 1992).

All interior tree species produce seed, with frequency and quantity being highly variable both within and among particular species. Aspen and birch exhibit typical characteristics of pioneering species, frequently producing large quantities of seed, at a relatively young age, and with the ability to disperse great distances (Zasada 1986). This strategy allows for rapid invasion of a newly disturbed site. White spruce produce episodic bumper seed crops, up to 12 years apart, but with limited dispersal (Zasada and Gregory 1969, Zasada 1971, Coates et al. 1994, Zasada 1995). White spruce bumper crops may be initiated by climatic conditions, including warm, dry weather, associated with large fire years, allowing exploitation of newly disturbed sites (Lutz 1956, Zasada 1971, Viereck 1973, Rupp et. al. 1997). Unlike white spruce, black spruce cones are semiserotinous, allowing for both yearly production and long-term retention of seed. Haavisto (1975) reported retention of cones for as long as 25 years. Black spruce is therefore able to maintain a seed bank within the overstory. A portion of the serotinous cones are able to survive all but the most severe wildfires, releasing seed onto the disturbed site and allowing for stand replacement to occur. It should be noted, that with the possible exception of paper birch, there is no significant soil seedbank for boreal forest trees (Perala and Alm 1990, Zasada et al. 1992).

Each of these strategies allows particular species to exploit specific post-disturbance conditions. The seed rain and environmental factors influencing the

seedbed are important controls to successful seedling establishment. The timing, quantity and quality, and effective dispersal distances of the seed crop are important seed rain issues that directly affect subsequent establishment of seedlings. These issues will be described in Chapter 3 for white spruce.

Vegetative reproduction is important in both primary and secondary succession (Zasada et al. 1992). This strategy allows an individual plant to take advantage of an established root system, and immediately exploit post-disturbance conditions. Paper birch employs basal buds as its chief vegetative source for regeneration, whereas aspen utilizes adventitious root buds to vigorously resprout following disturbance. The relative success of both these strategies is directly influenced by the type and severity of disturbance. For example, severe fires may damage or kill the bud bank resulting in an inability to produce vegetative stems on the disturbed site. Layering is an important cloning strategy of black spruce throughout its range, but is limited to treeline situations in white spruce (Viereck 1979).

Some species employ both sexual and vegetative strategies, such as paper birch and aspen, whereas white spruce reproduces sexually, except for layering at treeline. These strategies may occur simultaneously within a site and the relative importance of each in recolonizing the site will depend upon species composition, site conditions, and severity of disturbance (Zasada et al. 1992). Detailed descriptions of these strategies for boreal forest species can be found in Zasada (1971, 1986) and Zasada et al. (1992). Although this discussion was restricted to examples of tree species, it should be noted

that herb and shrub species strategies are also important, particularly with regards to species competition and forest establishment. These strategies include, the vegetative strategy of rhizomes employed by Calamagrostis spp. and Epilobium spp. and the sexual strategy of buried seed employed by Rubus spp. (Lieffers et al. 1993).

Both the disturbance regime and reproductive strategy are particularly important with regards to both the establishment and vegetation patterns of the Alaskan boreal forest. For example, in the fire dominated uplands, the reproductive strategies employed by individual tree species allow for maximum exploitation of the disturbed site and initiation of a new cohort upon the landscape. The successional pathways reflect this interaction and result in the vegetation mosaic of the Alaskan boreal forest (Viereck 1973, Van Cleve and Viereck 1981, Yarie 1981, Van Cleve et al. 1991). Synthesizing information regarding both the disturbance regime and reproductive strategy of species within a given ecosystem can provide information important in determining resultant successional pathways.

Successional Pathways

Successional pathways describe and predict the temporal sequence of species that may invade and/or dominate a site newly formed or disturbed. This sequence of "change" can be described with regards to other ecosystem characteristics such as biomass, productivity, and diversity (Odum 1969, Connell and Slatyer 1977, Denslow 1980). Such pathways are important in understanding the factors and mechanisms

which influence vegetation establishment and pattern. There has been much debate of the concept of forest succession, since first put forth by Thoreau in 1863 (Spurr 1952).

The first studies to observe and describe species replacement took place almost a century ago (Cowles 1899, Cooper 1913, Clements 1916). Clements' relay floristics model viewed succession as a sequential phenomenon, whereby the dominant species modifies and changes its environment making it more favorable for invading species (Clements 1916, 1928). Egler (1954) building on the work of Gleason (1926, 1927, 1939) proposed the initial floristic composition model. Egler's model viewed succession as the consequence of different rates of growth of the different species that are initially present at a site (McCook 1994). Egler's individualistic approach thus differed from Clements's "superorganism" concept.

Odum (1969) viewed ecological succession as the development of ecosystems. He presented a tabular model that identified successional trends, such as community energetics and structure, life history, and nutrient cycling, to be expected in the development of ecosystems. Drury and Nisbet (1973) developed a life history based successional model. They proposed "the basic cause of the phenomenon of succession is the known correlation between stress tolerance, rapid growth, small size, short life, and wide dispersal of seed." (Drury and Nisbet 1973, p. 360).

Connell and Slatyer (1977) proposed the three alternative mechanisms model of succession. They presented three pathways of successional change following disturbance. Model 1, facilitation, follows Clements's general idea that "presence of

later-successional species is dependent upon early ones preparing a favorable environment for them ..." (Connell and Slatyer 1977, p. 1136). Model 2, tolerance, proposes that succession leads to a community composed of those species most efficient in exploiting resources (Connell and Slatyer 1977). Model 3, inhibition, states there is no competitive advantage, but that the initial colonizer occupies the site over all other species. Simply by life-history characteristics, long-lived species dominate (Connell and Slatyer 1977).

Tilman (1985) presented his resource-ratio hypothesis of succession. The resource-ratio model contends that succession results along a gradient through time in the relative availability's of limiting resources and that succession is a directional and repeatable process, within the context of a resource-supply trajectory that is repeatable or directional (Tilman 1985). Therefore, species are specialized, with regards to resource limitations, and a community will reflect this specialization and change as resource supply change.

The above review highlights the major successional paradigms of the past century. These models continue to be debated, but each offers a theoretical basis for investigating factors and mechanisms responsible for establishment and vegetation changes.

General successional pathways and patterns have been investigated and described for interior Alaska floodplain and upland systems (Viereck 1970, Van Cleve and Viereck 1981, Foote 1983, Walker et al. 1986, Viereck 1989, Powers and Van

Cleve 1991, Viereck et al. 1993a). The seminal work of Van Cleve and Viereck over the past 30 years has produced a detailed understanding of the controls and mechanisms that drive succession in interior Alaska. Their model of floodplain succession (Viereck et al. 1993a) follows the traditional facilitation view, where successive dominant species alter the environment by shifting dominance to another species (Clements 1916, 1928, Connell and Slatyer 1977). The upland model follows the initial floristic composition or tolerance view (Egler 1954, Connell and Slayter 1977), where species establish simultaneously but dominate at different times due to differences in growth rates and life history traits. Yarie (1983) applied this paradigm to describe successional trends of the Porcupine River drainage, an area of over 3,600,000 hectares.

Upland, fire-dominated white spruce ecosystems are the focus of this modeling study. Detailed descriptions of these systems can be found in the literature (Van Cleve and Viereck 1981, Powers and Van Cleve 1991, Van Cleve et al. 1991, 1996). The sequence follows seven stages progressing from a newly burned site to a mature white spruce stand. Van Cleve et al. (1996) identified critical turning points between Stages I and II (newly burned to herb-tree seedling); Stage IV (dense hardwood); Stage V (mature hardwood); between Stage V and VI (mature hardwood to mixed hardwood and white spruce); Stage VII (mature white spruce and moss). The model presented here will focus on Stages I and II.

The idea of multiple successional pathways has received increased attention within the literature (Cattelino et al. 1979, Abrams et al. 1985, Youngblood 1992, Fastie 1995). Matthews (1979) identified the potential for multiple successional patterns, associated with a chronosequence, due to spatial-temporal environmental gradients of the site. Therefore, factors such as type, severity and frequency of disturbance, seed source availability, and microclimate, can result in multiple successional trajectories. Walker and Chapin (1986) and Walker et al. (1986) found this to be true for floodplain ecosystems on the Tanana River. These studies identified the stochastic nature of disturbance to be the driving force behind the general pattern of succession. The model of forest succession by Van Cleve and Viereck was found to be restrictive in describing successional relationships resulting from disturbances other than stand-replacing fires (Walker et al. 1986, Walker and Chapin 1986, Youngblood 1992).

The idea of multiple successional pathways, due to spatial-temporal environmental gradients of the site, provides a framework for investigation of factors and mechanisms that may cause deviation from the general pathway of upland white spruce given by Van Cleve and Viereck (1981) and Van Cleve et al. (1991). I explore these potential deviations through the modeling work presented. I identify key driving factors during early establishment (Stages I and II), such as disturbance effects and seed availability, that support this idea of multiple trajectories. Key environmental factors and ecological processes interact with the developmental history of a system to

cause deviant trajectories in the general pathway. The result is the mosaic pattern of vegetation observed across the landscape of interior Alaska.

Environmental Factors

Climate

Climate is the most important environmental factor controlling development and establishment of northern latitude forests. Van Cleve et al. (1991) discussing the state factors in the Alaskan boreal forest state, "The coldness of this northern environment dominates all physical, chemical, and biological processes." The general climate of the boreal forest is characterized by strong seasonal variation in which summers are short, moderately warm, and moist, and winters are long, extremely cold, and dry (Rumney 1968, Lydolph 1977, Larson 1980, Bonan 1988). The continental climate of interior Alaska provides an excellent example of this extreme seasonal variation.

Within the Fairbanks area, mean daily temperatures range from -24.5° C in January to 17.5° C in July, with an average annual temperature of -3.5° C (Van Cleve et al. 1991). The area is classified semiarid with potential evapotranspiration (PET) of 466 mm (Patric and Black 1968). The Fairbanks area lies within a rain shadow created by the Alaska Range, and receives an average of 285 mm of precipitation, of which 65 percent falls during the growing season (Viereck et al. 1993b, Van Cleve et al. 1991). The growing season has an average of only 97 frost-free days (Slaughter and Viereck 1986). The landscape is covered by snow for 6-7 months each year from mid-October

to April, with average maximum seasonal snow depth of 75 cm attained by February (Viereck et al. 1993b). The water equivalent of the snowpack is 11 cm (Viereck et al. 1993b). According to Thornthwaite (1948) there is little or no water surplus (Viereck et al. 1993b). Due to its high latitude, the Alaskan boreal forest has variable insolation with season. At Fairbanks, winter solstice has a maximum sun angle of only 1° 42', but at summer solstice maximum sun angle reaches 48° 42' (Viereck et al 1993b). Viereck et al. (1993b) describe climate on the Tanana River floodplain during the summer months. Uplands are similar to floodplains in regional climate (Van Cleve et al. 1991), but may experience more precipitation and lower air temperature.

It is under this climate regime that forest establishment and development occur. Furthermore, biota and topography modify climate to produce dramatic microclimatic differences. These differences affect the establishment process through their influence on key factors and processes, such as frequency and severity of disturbance, forest floor structure, and seed production.

Topography

The topographic modification of regional climate has dramatic consequences for ecosystem processes (Van Cleve et al. 1991). Due to low sun angle, aspect has substantial affects on vegetation patterns, nutrient cycling, permafrost, and disturbance characteristics (Van Cleve et al. 1991, 1996). The boreal forest recieves extremes in

seasonal insolor radiation During wintertime inversions, temperatures may increase by 10° C with an increase in elevation of 150 m (Youngblood 1992).

Topography directly influences the structure and function of the boreal forest. For example, the distribution of white and black spruce ecosystems are strongly tied to aspect which mediates microclimate, forest floor structure, and decomposition. The various topographic components of aspect, slope, and elevation interact in complex ways with other state factors and ecosystem controls, to produce the dramatic differences in ecosystem processes and vegetation patterns characteristic of the boreal forest landscape. These effects impact several driving factors and processes of forest establishment including climate, disturbance, forest floor structure, edaphic factors including soil drainage and permafrost, and seed dispersal across the landscape. Besides modification of regional climate, the most important influence of topography is its role as being the major determinant of disturbance frequency and intensity and the post-disturbance microclimate that is produced.

Disturbance

Disturbance by fire, fluvial processes, insects and disease, snow and wind breakage, and small and large mammal herbivory are all important mechanisms driving succession in the boreal forest. However, in the uplands, wildfire is the most common and pervasive component of the disturbance regime producing much of the vegetation mosaic across the landscape. It is this component and the subsequent establishment

patterns which the model ABFEM simulates. Therefore, it is important to review the major effects of wildfire on the structure and function of upland forest ecosystems. I will highlight only the effects that are most important to the model.

Fire in interior Alaska, as well as in most fire-dominated systems, is heterogeneous in its impact on ecosystems; producing a spatially variable pattern in both areal extent and the intensity/severity of its effects (Lutz 1956, Quirk and Sykes 1971, Viereck 1973, Heinselman 1981, Thomas and Wein 1985, Hobbs and Atkins 1988, Ratz 1995). Furthermore, the effect of fire, within the context of relationship between intensity/severity and post-fire vegetation structure, is spatially variable at multiple scales (Dyrness and Norum 1983, Zasada et al. 1983, Eberhart and Woodward 1987, Baker 1993). This spatial heterogeneity is evident in all aspects of the post-fire landscape of interior Alaska; the vegetation structure, forest floor thickness, microclimate, soil chemistry, microbial community, and active layer of permafrost sites all exhibit effects of this spatial heterogeneity.

Except for surviving islands and stringers, fire in the Alaska boreal forest destroys the overstory vegetation and significantly alters, to various degrees, the structure and function of the forest floor. Functional and structural aspects of the forest floor have been studied extensively in the Fairbanks area (Viereck and Dyrness 1979, Viereck et al. 1979, Viereck 1982, Dyrness and Norum 1983, Viereck and Foote 1985, Dyrness et al. 1986, Dyrness et al. 1989). Post-fire increases in pH, nutrient availability, microbial populations and associated nutrient cycling, active layer of

permafrost sites, light, and soil temperature all provide a favorable but highly variable environment for seedling establishment and growth. The post-fire forest floor structure interacts with these favorable conditions to influence establishment patterns upon the landscape.

Fire affects the establishment potential of seedlings by altering factors such as forest floor thickness, competitive ability of survivors, and the soil seed bank potential. These characteristics of the seedbed exhibit a causal relationship to successful seedling establishment (Zasada et al. 1983, Fox et al. 1984, Thomas and Wein 1985, Putnam and Zasada 1986, Walker et al. 1986, Zasada et al. 1987). Youngblood (1992) investigated differences in the pattern of white spruce invasion between aspen and paper birch stands, finding that in some cases colonization of aspen stands can be delayed for a significant number of years due to lack of adequate light and growing space created by heavy litterfall and high aspen stem density. Therefore, seedling establishment potential can be viewed from the point of initial post-fire seedbed availability that declines as the site becomes occupied by other vegetation. Seedbed characteristics can be linked with important ecological processes, such as seed production and dispersal and vegetative regeneration, to simulate potential post-fire establishment of tree seedlings upon the landscape.

Ecological Processes

Cone and Seed Production

Natural regeneration from seed is an important component within the reproductive strategies of all interior Alaska tree species. As discussed previously, some species such as aspen and paper birch utilize both sexual and vegetative reproduction, whereas white spruce reproduces almost exclusively by seed. Therefore, production of white spruce cones and subsequent seed are critical to their post-disturbance establishment success. Seed production is also important to aspen and birch, as a means of colonizing a new site or a site where fire was severe enough to prevent vegetative regeneration, but where pre-disturbance communities existed, vegetative means can also be employed in recolonization.

Interior Alaska white spruce cone and seed production is episodic (Waldron 1965, Zasada and Viereck 1970, Eis and Inkster 1972, Zasada 1980, Zasada et al. 1992, Youngblood and Max 1992). Meteorological factors, such as a warm, dry summer, initiate good crops (Lutz 1956, Zasada and Gregory 1969, Zasada 1971, Viereck 1973, Alden 1985, Coates et al. 1994). Bumper crops have been observed in the Fairbanks area to occur at intervals of up to 12 years, with 28 years separating the exceptional crops of 1958 and 1987 (Zasada and Viereck 1970). Such long periods between crops have great implications on the ability of a cohort to become established on a disturbed site. Furthermore, the timing of such crops can greatly influence the successional pathway of a site (Zasada et al. 1992, Zasada 1995). White spruce seed

viability varies considerably, both temporally and spatially. Spatial variability occurs at all scales, from the individual tree- to the landscape-level. In general, high cone production events are associated with high viability, 45 to 85 percent, and low cone production events with low viability, 0 to 45 percent (Waldron 1965, Zasada and Viereck 1970, Zasada et al. 1978, 1992, Fox et al. 1984, Coates et al. 1994). Factors affecting seed quality include availability of pollen, growing-season temperatures, and attacks by pathogens and insects (Alden 1985). The topic of white spruce cone and seed production will be discussed in detail in Chapter 3. Implications that the frequency, quantity, and quality of seed produced has upon post-disturbance establishment patterns will be discussed in Chapters 4 and 5.

Production of paper birch seed is also variable, but not to the degree of white spruce. Paper birch seed production shows great variability from year to year, but exhibits a somewhat predictable pattern (Perala and Alm 1990). In northern Wisconsin, Godman and Mattson (1985) noted the production of good seed crops 1 year in 4, with poor crops occurring 2 years in 5. Bjorkbom et al. (1965) noted the occurrence of a medium or better crop every other year in the Lake States and New England. Zasada and Gregory (1972) found seed crops adequate for natural regeneration of 30.5-meter-wide clearcuts occur at least 1 out of 4 years in interior Alaska. The quantity and viability of seed produced by these crops also varies significantly, both temporally and spatially. In general, seed viability is low, but in terms of total viable seed produced is large compared to white spruce (Bjorkbom 1971,

Zasada and Gregory 1972, Perala and Alm 1990). The birch seed crop classification of Marquis (1969) suggested 121 viable seeds/m^2 associated with a poor rating. Within the model ABFEM, a white spruce cone crop producing 121 viable seeds/m^2 would be considered a moderate crop. For pure even-aged paper birch stands in interior Alaska, Zasada and Gregory (1972) observed within stand total seedfall to range from 542 to 72,805 seeds/m^2 over a 5 year period. Numerous other observations of birch seed production exist in the literature (Bjorkbom 1971, Zasada 1971, Godman and Mattson 1976, Archibold 1980, Perala and Alm 1989, Zasada et al. 1992).

Aspen is a frequent and prolific seeder. Godman and Mattson (1976) observed 6 successive good or better seed crops. Lutz (1956) cited a study in northern Europe that reported aspen total seed production of between 162 and 202 million seeds per acre. Maini (1972) reported the production of 1.6 million total seeds from a single 23-year-old trembling aspen in southern Ontario. Little information is known about interior Alaska aspen seed production. However, Zasada et al. (1992) cited some unpublished data for interior Alaska reporting common aspen seed rain of 571 total seeds/m^2.

Seed Dispersal

The dispersal of seed upon the landscape directly influences subsequent seedling establishment patterns. Some species, such as white spruce, depend almost solely upon seed to recolonize a disturbed site (Zasada 1972, 1995). The pattern of seed dispersal

or the "seed shadow", as defined by Janzen (1971), describes the spatial distribution of seed about its source. Harper (1977) suggested that the pattern of colonization was a function of the seed shadow. Coupling information about cone and seed production with information about the dispersal of seed onto the landscape provides a powerful tool for predicting the regenerative potential of a site. ABFEM simulates this dispersal process for interior Alaska white spruce and paper birch seed.

White spruce seed is dispersed primarily by wind. Some debate exists about the importance of secondary wind dispersal of seed across snow (Dobbs 1976, Zasada 1995, Greene and Johnson 1995). The distance and density of seed dispersed is influenced by the terminal velocity of the seed, height of release, wind speed and turbulence, and species specific morphological traits related to dispersal (Augspurger and Franson 1987). Several studies have found dispersal distances of up to 475 m, with the majority observing maximum dispersal distances of 200 to 300 m (Rowe 1955, Schlesinger 1970, Dobbs 1976, Zasada and Lovig 1983, Zasada 1985, Youngblood and Max 1992, Greene and Johnson 1995). Youngblood and Max (1992) reported little potential for seedling establishment beyond 100 m on Willow Island in interior Alaska. These studies agree with the general dispersal pattern, one fitting the negative exponential model, typical of the majority of tree species (Harper 1977, Okubo and Levin 1989, Willson 1992a, 1992b, Farmer 1997). This limited dispersal distance and acute decline in seed density as distance from the source increases has important

implications for the regenerative potential of white spruce on disturbed sites. The topic of white spruce seed dispersal in interior Alaska will be discussed in detail in Chapter 3.

Paper birch is also dispersed by wind. Birch seed is dispersed throughout the year with the majority dispersing from September through November, allowing for some secondary wind dispersal across a snowpack (Bjorkbom et al. 1965, Bjorkbom 1971, Matlack 1989, Safford et al. 1990). Matlack (1989) found that secondary dispersal of *Betula lenta* seed increased the area covered by primary wind dispersal by a factor of three. Paper birch dispersal patterns follow the general pattern of the negative exponential model (Perala and Alm 1990). In Maine, Bjorkbom (1971) found birch seedfall densities at the stand edge to be 58 percent of within stand seedfall densities. At 54 m from the stand edge seedfall densities were 10 percent of within stand densities. On a newly burned site in interior Alaska, Zasada (1985) observed as high as 40 percent of within stand seedfall at 50 m, but less than 10 percent at 100 m from the stand edge. Although quantity and frequency of birch seed are substantially better than white spruce, the quality or viability of birch seed can be significantly lower than spruce for a given year (Zasada et al. 1992). The large variability in seed viability can play an important role in seedling establishment (Bjorkbom 1971, Zasada and Gregory 1972, Zasada 1985).

Seedling Establishment

The establishment of seedlings from seed is a complex process (Grubb 1977, Harper 1977, Zasada 1986, Zasada et al. 1992). Seedling establishment is a function of the quantity and type of reproductive material, the nature and severity of disturbance, and species specific growth requirements (Zasada et al. 1992). Harper (1977) described three components to the process of natural regeneration : (i) seed production, (ii) the seed bank, and (iii) the environment, which encompasses all the biotic and abiotic variables acting upon the germination, survival, and growth of seedlings. The most successful germination and growth of boreal forest tree species occur on exposed mineral soil seedbeds (Zasada 1986).

White spruce seedling establishment success hinges upon the availability of a receptive seedbed. In general, white spruce establishment success is highest on mineral soil seedbeds (Zasada and Gregory 1969, Zasada 1971,1972,1986, Zasada et al. 1992). Such seedbed conditions are associated with the effects of fire upon the forest floor (Viereck and Dyrness 1979, Viereck et al. 1979, Viereck 1982, Dyrness and Norum 1983, Viereck and Foote 1985, Dyrness et al. 1986, Dyrness et al. 1989). This small window of opportunity, in terms of a receptive seedbed, must coincide with the production of seed for the establishment of a cohort to be realized. The use of seed:seedling ratios, which determine the number of seeds needed to produce a seedling of a given age, can provide a general measurement of the difficulty of establishment (Zasada et al. 1992). Roe et al. (1970) developed a regeneration triangle

to describe Englemann spruce regeneration requirements in the Rocky Mountains. The three main requirements are: (i) an adequate seed supply, (ii) a favorable seedbed for germination, and (iii) a suitable microenvironment for survival and growth (Roe et al. 1970, Coates et al. 1994).

Paper birch seedling establishment requirements are much the same as for white spruce. Paper birch seedling establishment success again hinges upon a receptive seedbed. Mineral soil conditions provide the most receptive seedbeds (Lutz 1956, Zasada et al. 1978, Perala and Alm 1990). Lutz (1956) found these conditions created by fire to be optimal for paper birch regeneration. The more regular production of paper birch seed compared to white spruce enables paper birch to realize the establishment "window" with greater frequency.

Establishment of aspen seedlings from seed is dependent upon several requirements occurring in the short-lived period of seed viability. Seeds must germinate within a few days to weeks of dispersal (Schreiner 1974, Zasada et al. 1992). The most notable requirement is the availability of a moist, mineral soil seedbed during the short viability period (Maini 1960, 1968, Peterson and Peterson 1992). The probability of these stringent conditions being available upon a recently burned site is uncommon (Maini 1960, 1968, 1972). For these reasons the majority of the literature focuses on vegetative reproduction (Peterson and Peterson 1992). Although, Peterson and Peterson (1992) cite research identifying seedling reproduction from seed in the development of aspen stands, the majority of aspen regeneration is by root suckers.

Therefore, the model will represent only the vegetative strategy of suckering. It should be noted that Zasada et al. (1977) suggested that seedling reproduction from seed may be of greater importance in the northern part of its range, such as Alaska, due to the colder soil conditions. Colder soils may mediate the effects of fire, in terms of available soil moisture, and provide the germination requirements needed by aspen seed. Further investigation of this issue, as well as basic production and dispersal information for interior Alaska, is needed before seedling establishment from seed can be accurately represented by the model.

Vegetative Regeneration

Vegetative reproduction is an important regeneration strategy in secondary succession (Zasada et al. 1992). This strategy allows an individual plant to take advantage of an established root system, and immediately exploit post-disturbance conditions. Paper birch and aspen both employ vegetative reproduction in colonizing a disturbed site. Whereas white spruce, except for layering at treeline (Viereck 1979), is dependent upon seed from neighboring seed sources to colonize a site. The relative success of vegetative reproduction is directly influenced by the type and severity of disturbance.

Paper birch produces stump sprouts from dormant basal buds. Paper birch begin to lose their ability to sprout after 40-60 years (Perala and Alm 1990, Safford et al. 1990, Zasada et al. 1992), however Safford et al. (1990) reported that 60 percent of

paper birch at age 140 still produced sprouts in interior Alaska. Except following a severe fire, where dormant basal buds may be consumed, disturbance that causes overstory mortality will result in sprouting (Perala and Alm 1990, Zasada et al. 1992). Empirical data on the density of paper birch stump sprouts following fire in interior Alaska is lacking.

Aspen is a prolific root sprouter. Aspen produces shoots from adventitious buds developed on the root system (Zasada et al. 1992). Root suckering in aspen is triggered by elimination of apical dominance (Weber 1990), such as fire induced mortality. Furthermore, the soil within rooting depth must be warmed to 18^0 to 35^0 C, 24^0 C being optimal, by solar radiation for suckering to be initiated (Maini and Horton 1966, Gifford 1967, Perala 1974). The majority of suckering originates from fine roots (0.5 to 2.5 cm) and at depths of 4 to 12 cm below the soil surface (Peterson and Peterson 1992). Severe fires have been observed to kill a majority of shallow roots, resulting in little or no suckering (Perala 1974, Schier and Campbell 1978, Peterson and Peterson 1992). Brown and DeByle (1989) observed low intensity fires, characterized by little overstory mortality and the presence of competition and high shade, did not result in suckering. Reports of sucker densities one year following harvesting range from 44000 to 225000 stems per hectare, with a density range of 20000 to 25000 stems per hectare at age six (Peterson and Peterson 1992).

Rapid vegetative reproduction of paper birch and aspen decreases the ability of seeds to germinate and establish on occupied sites. Sprouting acts as a major competitive force with regards to white spruce establishment (Youngblood 1992).

Summary

This chapter provides an overview of the developmental history and key environmental factors and ecological processes important to the early post-disturbance establishment patterns of white spruce ecosystems in interior Alaska. The conceptual model (Figure 2-1) portrays important factors and mechanisms that influence the spatial/temporal establishment patterns of these systems. This conceptual model served as the theoretical foundation for the development of the geographic model ABFEM. The conceptual model was designed to represent a simplistic view of the factors and mechanisms driving the establishment process. The factors and processes represented in the conceptual model will be described in detail in Chapter 4.

The objective of the conceptual model was to provide an ecological and theoretical foundation, that would serve as the basic framework for development of the geographic model. A key component of this process was to provide only the most simplistic view of the establishment process, in terms of representation of factors, mechanisms and processes. This allowed the model to simulate and represent only the most basic driving variables; providing for a systematic exploration of the early post-disturbance establishment process of interior Alaska forests. A detailed description and

analysis of this exploration process is presented in Chapters 4 and 5, as well as a discussion of future model development and analysis in Chapter 6.

The developmental history of a forest ecosystem provides a general context in which a system develops. The disturbance regime affects and interacts with plant strategies to drive succession. The specific combinations of these developmental history attributes (i.e. disturbance regime, successional pathway, and plant strategy) influence the spatial and temporal gradients of key environmental factors (i.e. climate, topography, and disturbance effects) and ecological processes (i.e. seed production and dispersal and seedling survival and growth) to produce deviants within the general successional pathway of the ecosystem. Such multiple pathways, conditioned by gradients in climate, disturbance effects, and topography, produce different forest establishment patterns across the landscape. When these factors are coupled with information on seed production and dispersal and then represented geographically, a powerful tool is assembled. This tool, the model ABFEM, provides both predictive and investigative capabilities for the study of forest establishment patterns in the Alaskan boreal forest.

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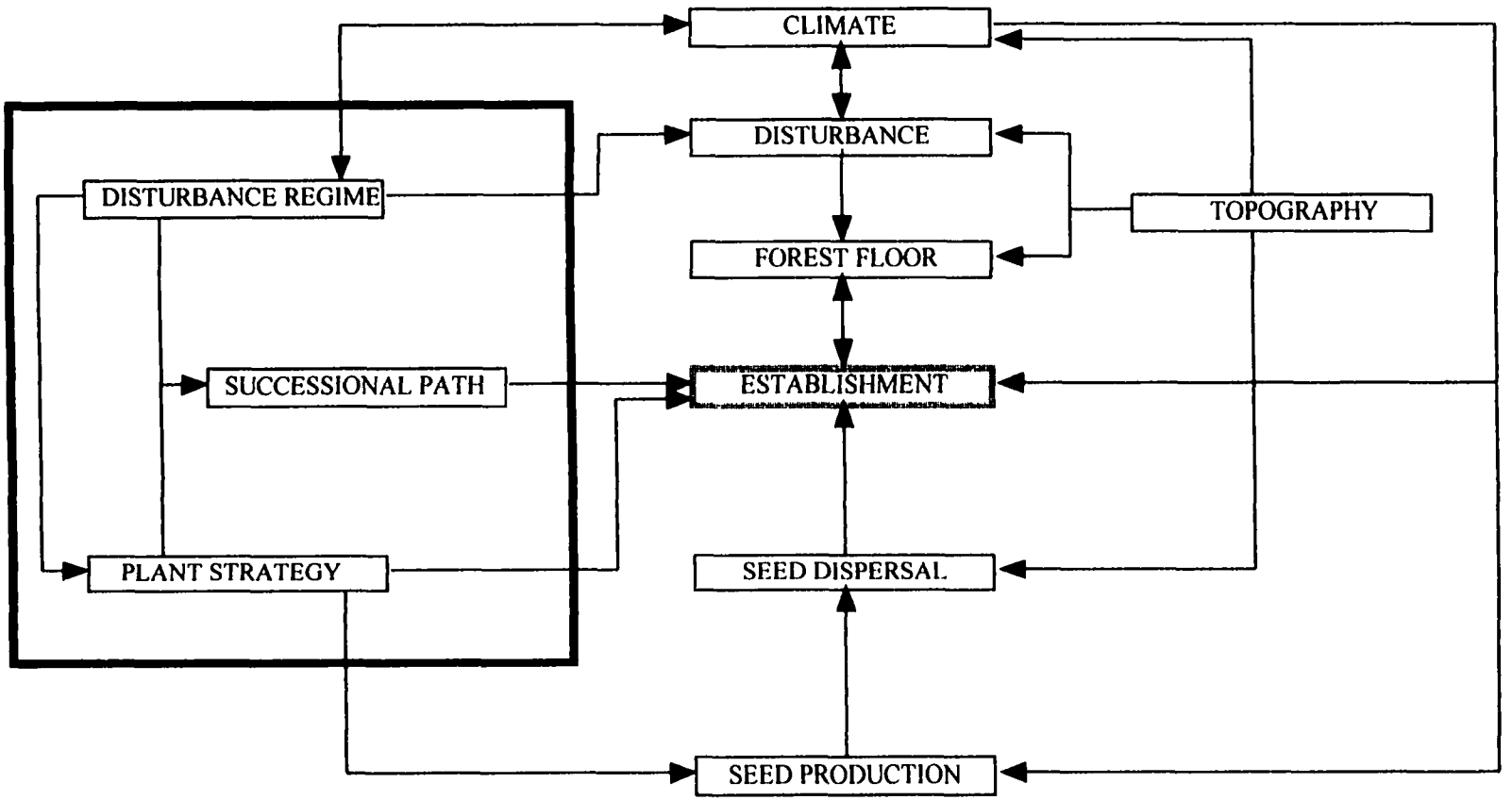

Figure 2-1. Conceptual model of key environmental factors and processes driving forest establishment following disturbance. Heavy boxed components represent developmental history attributes.

CHAPTER 3 - OBSERVATIONS ON THE DISPERSAL OF WHITE SPRUCE SEED ACROSS INTERIOR ALASKA

Introduction

The production and dispersal of seed are fundamental to the natural regeneration process. Regeneration via seed allows for both the continuation and establishment of communities, is responsible for change in floristic composition of communities, and provides genetic variability for species adaptation (Farmer 1997). The episodic nature of white spruce cone and seed production and limited dispersal ability (Zasada and Gregory 1969, Dobbs 1976, Zasada and Lovig 1983, Zasada 1985, Youngblood and Max 1992) raises questions as to its ability to persist naturally on the landscape. In interior Alaska white spruce is an important component of the boreal forest. The persistence and management of white spruce are critical to maintaining sustainable ecosystems. Increasing understanding of the production and dispersal of white spruce seed will assist land managers in moving closer toward realizing ecosystem sustainability.

The reproductive cycle of white spruce is well documented (Zasada and Gregory 1969, Dobbs 1972, Nienstaedt and Teich 1972, Owens and Molder 1984, Alden 1985, Nienstaedt and Zasada 1990). The production of seed is a 17 to 18 month process beginning with bud initiation in late April and ending with dispersal of seed in September the following year. The reproductive process involves several stages

including bud differentiation, flowering and pollination, and seed maturation, which all respond to certain environmental and physiological factors and events. The response to these events and factors determines the success or failure of a particular cone and seed crop.

Rupp et. al. (1997) investigated the apparent synchrony between white spruce reproduction and climatic and tree physiological factors, identifying several "critical gateways" that must be passed for a cone crop to be realized. Meteorological factors, such as a warm and dry growing season the year prior to seed dispersal, appear necessary for the initiation of a cone crop (Lutz 1956, Fraser 1958, Matthews 1963, Waldron 1965, Zasada and Gregory 1969, Zasada 1971a, Eis and Inkster 1972, Viereck 1973, Alden 1985, Zasada et al. 1992, Coates et al. 1994). Frost during flowering and rain during the pollination period may also affect the overall success of a seed crop (Zasada 1971a, b). Several studies have identified statistically significant relationships between cone production and meteorological factors for other conifer species (Lowry 1966, van Vredenburch and la Bastide 1969, Eis 1973).

A tree physiological response, produced by the previous years crop, has been shown to reduce the number of available sites for differentiation of reproductive buds, therefore excellent years are commonly followed by poor years (Matthews 1963, Zasada et al. 1992, Farmer 1997). Rupp et. al. (1997) found a response of decreased radial growth of interior Alaska white spruce trees in years of successful cone and seed production, suggesting a cost of reproduction that competes directly with growth.

Successful production events are dependent upon the tree's current physiological condition and generally do not occur during periods of depleted tree growth reserves (Rupp et. al. 1997). Individual tree response is variable, reflecting differences in individual tree nutrition, site conditions, canopy position, and environmental factors (i.e. drought or insect attack). Investigation of the relationship between cone and wood production for other conifer species has also shown a decrease in ring width during years of high cone production (Daubenmire 1960, Eis et al. 1965).

The dispersal of seed onto the landscape directly influences seedling establishment patterns. The distance and density of seed dispersed is influenced by the terminal velocity of the seed, height of release, wind speed and turbulence, and species specific morphological traits related to dispersal (Augspurger and Franson 1987). Dispersal of seed from an area source can be described by the negative exponential model (Okubo and Levin 1989, Willson 1992, Farmer 1997). The density of seed decreases sharply as distance from the seed source increases. This "seed shadow", as defined by Janzen (1971), describes the spatial distribution of seed about its source.

White spruce seed is dispersed primarily by wind. Some debate exists about the importance of secondary wind dispersal of seed across snow exists (Dobbs 1976, Zasada 1995, Greene and Johnson 1995). For interior Alaska, the majority of seed is dispersed in September and October before permanent snow cover (Zasada and Viereck 1970, Zasada et al. 1978, Youngblood and Max 1992). Several studies have investigated white spruce seed dispersal into clearings (Rowe 1955, Schlesinger 1970,

Dobbs 1976, Zasada and Lovig 1983, Zasada 1985, Youngblood and Max 1992, Greene and Johnson 1995). White spruce has been reported to have a limited dispersal range, with few seeds being dispersed beyond 200 to 300 m from the source edge (Zasada and Gregory 1969, Dobbs 1976, Zasada and Lovig 1983, Zasada 1985, Youngblood and Max 1992). Greene and Johnson (1995) measured seed up to 475 m from the seed source and modeled potential long distance (i.e. > 300 m) wind dispersal of seed across the landscape. Although winds are important to the dispersal of seed, the effects of prevailing wind patterns upon the seed shadow are inconclusive (Harris 1967, Schlesinger 1970, Zasada and Lovig 1983, Youngblood and Max 1992, Greene and Johnson 1995, 1996). Understanding white spruce seed dispersal patterns across the landscape and factors responsible for these patterns would provide important information regarding potential seedling establishment patterns.

The processes of seed production and dispersal are critical components to forest management and natural regeneration. A better understanding of white spruce seed availability, both production and dispersal, would provide increased confidence to the land manager for implementing natural regeneration methods in white spruce management (Zasada 1995). Furthermore, a better understanding of these processes may provide answers to broader questions of environmental synchrony and persistence in the environment.

The objective of this chapter is twofold. First, to report measured seed production and viability of several seed source locations sampled within interior

Alaska. Second, to report measured seed dispersal patterns across the landscape from distinct seed sources and at various locations throughout interior Alaska.

Methods

Study sites

The study involved four regional areas within interior Alaska (Figure 3-1). Three treeline regions were selected, one region representing latitudinal treeline and two representing elevational treeline. The fourth region represents a typical upland white spruce site. Treeline sites were included to investigate possible differences in dispersal patterns, relative to upland or floodplain sites, and to provide information on the expansion of white spruce into new habitats, following disturbance and/or climate change.

A latitudinal treeline study area was established on the south side of the Brooks Range at the head of the Dietrich River valley. Due to the high latitude of the Brooks Range there is an interacting effect of both latitude and elevation upon treeline (Viereck 1979). Therefore, the latitudinal limit of white spruce is partially mediated by the altitudinal treeline constraint of the Brooks Range. Three distinct mature white spruce seed sources near treeline were selected. Site 1 (BR-1) was a northwest aspect stand (N 68^0 00' W 149^0 44') at an elevation of 610 m. Site 2 (BR-2) was a northwest aspect stand (N 68^0 01' W 149^0 43') at an elevation of 610 m. Site 3 (BR-3)) was a south aspect stand (N 68^0 02' W 149^0 41') at an elevation of 640 m.

One of two elevational treeline study areas was established in Denali National Park and Preserve on the north side of the Alaska Range. Two distinct mature white spruce seed sources near treeline were selected. Site 1 (DP-1) was a south aspect stand (N 63^0 44' W 149^0 02') at an elevation of 945 m. Site 2 (DP-2) was flat (N 63^0 43' W 149^0 09') with an elevation of 915 m. A second elevational treeline site was established at Twelve Mile Summit within the White Mountains of interior Alaska. The site (TS) was a southeast aspect stand (N 65^0 23' W 146^0 00') at an elevation of 885 m.

An upland study area was established in the Bonanza Creek Experimental Forest (BCEF), 20 km southwest of Fairbanks. A large mature white spruce stand, which survived the 1983 Rosie Creek fire, was selected. The BCEF site is a large oblong island running along a ridge with a southeast aspect (N 64^0 44' W 148^0 18') at an elevation of 265 m, surrounded by a large clearing created by the burn and subsequent salvage logging. Stand characteristics for the study sites are shown in Table 3-1.

Seed dispersal

Seed dispersal was measured using seed traps within and around the distinct, mature white spruce stands. At each site seed traps were located along transects running from within the stand to a given distance and direction away from the stand edge. The seed traps were 0.5 x 0.5 m wooden frames with a screened bottom and

lined with nylon netting. Hardware cloth covers were not placed on the top of the seed traps, allowing for natural predation. The traps were installed in July 1995.

For the Brooks Range sites, two parallel transects 10 m apart were established upslope from the source stand and two transects sideslope along the treeline edge of the stand. Due to topographic effects, the upslope transects represent a combination of elevational and latitudinal treeline. Whereas the sideslope transects represent an apparent latitudinal treeline, altered somewhat from a true northerly direction by physiographic features (i.e. position of mountain ridges and the Dietrich River valley). Ten seed traps were placed along each transect at -10, 0, 10, 20, 40, 60, 100, 150, 200, 300 m from the stand edge. Some distances had to be changed due to steep slope, a snowmelt outwash, and a mudslide.

In the Alaska Range, a transect was established perpendicular to each of the stand edges of each site in an upslope, downslope, sideslope right, and sideslope left direction. No downslope transect was established at DP-2, due to the presence of the park road. Ten seed traps were placed along each transect at -10, 0, 10, 20, 40, 60, 100, 150, 200, 300 m from the stand edge. Again some distances had to be changed due to steep slope, a large snowmelt outwash, and a creek.

In the White Mountains, two parallel transects 10 m apart were established running upslope from the source stand. No transects were established in a sideslope direction, due to the presence of a road. Sixteen seed traps were placed along each transect at -20, -10, 0, 10, 20, 30, 40, 50, 60, 80, 100, 150, 200, 250, 350, 450 m from

the stand edge. An additional 3 traps were placed within the interior of the stand in June of 1996.

At BCEF, 12 transects were established, running every 30 degrees from a point within the source stand into the burn (Figure 2). Fourteen seed traps were placed along each transect at -10, 0, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 150, 200 m from the stand edge. An additional 3 traps were placed within the interior of the stand. A few traps had to be removed due to their location upon roads.

Seed collection began in September 1995. Seed traps were emptied in late September and after snowmelt the following spring. After collection, total white spruce seed was counted. In 1996 the treeline sites were collected only once following snowmelt.

Seed viability

Average percent seed viability was measured for each site and year. At BCEF, the seed was stratified into fall and spring collected seed and then further stratified by distance interval ($\leq$ 20 m, 20 - 40 m, and > 40 m from the stand edge) for each collection date. Each sample contained 25 seeds. The germination tests were replicated four times with a control in each replicate. The controls consisted of 100 known high quality white spruce seeds collected in the Fairbanks area in 1987. Seeds were germinated in petri dishes lined with moist filter paper. Each replicate group was sealed in a plastic storage bag to provide more stable germination conditions (i.e.

temperature and humidity). A 14 day germination trial was conducted with daily recordings of germinated seed. Seed germination was determined by emergence of the radicle.

Statistical analysis

Descriptive statistics were used to compare seedfall and germination measurements at each site. The spatial distribution of total seed to distance from the nearest seed source was described through nonlinear regression of the data, employing a weighted negative exponential model. All seed trap distances were corrected to true horizontal distances for the regression analysis. Confidence intervals (95 percent) were calculated for the individual coefficients of each regression equation. The slope and intercept confidence intervals allowed comparison among site transects for similar shape (i.e. slope) and magnitude (i.e. intercept value). Transformation of the regression data, re-expressed as percent of within stand seedfall, allowed for general comparison among sites and identification of dispersal "thresholds" (i.e. the distance at which ≥ 25 percent of within stand seedfall is dispersed). Daily wind direction data from a weather station approximately 400 m from the BCEF upland stand was acquired for analysis of any potential relationship between dispersal pattern and wind direction. The weather station is part of the BNZ/CPCRW LTER site. A description of the weather station and wind measurement equipment can be found in Viereck et al.

(1993). Circular statistics following the methods of Fisher (1993) were employed to calculate the average wind direction at BCEF over a 26 day period in September.

Results

Seed dispersal

White spruce seed dispersal was measured for both the 1995 and 1996 seed crops. Seed dispersal, both density and spatial distribution, were variable among and within sites and between seed years (Table 3-2). In 1995 the production and dispersal of seed were measured at all the treeline sites, however the upland site at BCEF produced no cone or seed crop. In 1996 seed production and dispersal were measured at all sites.

Table 3-2 shows relatively low within stand seed production for the treeline sites for both years. The Alaska Range sites had a twofold or greater average seed density level than the Brooks Range sites. There was no 1995 seed crop produced at the BCEF site. The 1996 seed crop for the BCEF site averaged 139 total seeds/m^2 within the stand. The highest average density level outside the stand was 122 total seeds/m^2 at the stand edge. Maximum measured dispersal distance was 200 m, where an average of 19 total seeds/m^2 were dispersed. In the White Mountains, virtually no seed was dispersed beyond the stand edge in either year.

Nonlinear regression of seed density as a function of distance from the stand edge was performed. A majority of seed traps collected were empty. No regressions

were performed for the Twelve Mile Summit site, due to lack of seed collected beyond the stand edge. The limited number of observations made it impossible to perform regression analysis for three treeline sites.

In the Brooks Range a total of 201 seeds were collected in 1995, with 30.8, 25.9, and 43.3 percent total seed collected from BR-1, BR-2, and BR-3 respectively. In 1996 only 39 seeds were collected, with 12.8, 5.1, and 82.1 percent total seed collected from BR-1, BR-2, and BR-3 respectively. Only the BR-3 site received adequate seed for analysis purposes.

A comparison of regression coefficient confidence intervals (Table 3-3), shows variability among individual transects and years for the Brooks Range site (BR-3). The slope coefficient (b1) confidence intervals can be compared to identify similar shaped curves (i.e. overlapping confidence intervals). There is general agreement among all transects, except the BR-3B-95 and BR-3C-95 transects (Figure 3-3). These two curves showed a fundamentally different shape compared to the other regression curves.

Regressions were performed for both sites in the Alaska Range. A total of 205 seeds were collected in 1995, with 52.7 and 47.3 percent total seed collected from DP-1 and DP-2 respectively. In 1996 a total of 169 seeds were collected, with 47.9 and 52.1 percent total seed collected from DP-1 and DP-2 respectively.

A comparison of regression coefficient confidence intervals (Table 3-3), also shows variability among individual transects and years. Comparison of the slope

coefficient (b1) confidence interval reveals three different shapes for the DP1 site (Figure 3-4). No apparent trend among transects or years was observed, except slope agreement among three of the four 1995 transects. The DP2 site had two fundamentally different curves with all 1995 transects possessing a similar shape (Figure 3-5).

Due to lack of seed production, regression analysis was performed for the 1996 BCEF seed crop only. A comparison of regression coefficient confidence intervals (Table 3-4), shows variability among individual transects. Comparison of slope confidence intervals (b1) revealed three different curve shapes (Figure 3-6). The 120^0 and 300^0 transects had a fundamental difference in shape compared to the other transects. These two transects are located at either end of the long axis of the seed source, suggesting an influence of seed source orientation upon dispersal trends.

To investigate the potential influence of wind a nonlinear regression was applied to only those transects accounting for the majority of seed collected. The 180^0, 210^0, 240^0, and 270^0 transects accounted for 84 percent of the total seed collected. The majority of seed dispersal, 61 percent, was observed primarily between August 25 and September 19. The mean wind direction for this 26 day period was calculated to be 239 degrees. The transects were divided into leeward and windward, based upon the average wind direction for the period of observation and the orientation to the seed source (Figure 3-2).

The leeward transects (180^0, 210^0, 240^0, and 270^0) explained a greater amount of the variance than the windward transects. The leeward transects had an R^2 value of 0.31 versus 0.19 for the windward transects (Figure 3-7). There was a threefold difference in seed deposition between transects oriented with the wind versus against the wind.

Seed viability

Germination rates were low for all sites. The control samples had an average viability of 79 percent. Figure 3-8 shows the majority of seed germinated in the first 7 days. One treeline site had seed germinate, the 1995 DP2 site had an average viability of 4 percent. The low value reflects the literature (Zasada et al. 1992, Farmer 1997), with very low viability at treeline sites. Many of the treeline seeds developed molds by the end of the 14 day trial, suggesting possible immature seed or improper storage.

The BCEF site was stratified by collection date (fall or spring) and distance interval (≤ 20 m, 20 - 40 m, and > 40 m from the stand). Figure 3-9 shows an average viability of 15 percent, with a higher fall viability of 19 percent versus the spring viability of only 11 percent. There were no clear trends within the distance intervals.

Discussion

White spruce seed dispersal

Information on the dispersal of seed from a seed source into clearings has been collected for many species over the past 50 years (Harper 1977, McCaughey et al. 1986, Coates et al. 1994, Farmer 1997). The density of seed dispersed and the distance to which seed is dispersed is important silvicultural and ecological information. Such information provides the land manager with an idea of the potential for natural regeneration on a disturbed site. This information can be used to assist in harvest layout and management decisions, optimizing the chance for natural regeneration success.

Measurement of white spruce seed dispersal throughout interior Alaska showed that the majority of seed was dispersed near the edge of the seed source and a small portion of seed was dispersed some distance into clearings from the source stand. There was considerable variability among individual transects and between sites and regions. This suggests that the majority of dispersal studies in the literature over-generalize the relationship between seed deposition and distance from the seed source. A critical deficiency in these studies has been the location of dispersal transects, which are traditionally oriented with prevailing winds. Applying regression results to the entire stand in many cases will result in overestimation of seed deposition patterns across the landscape.

At treeline, dispersal curves varied considerably between individual site transects and among sites. The limited maximum dispersal distance of 20 m for the Twelve Mile Summit site illustrates the effect of wind and topography. Strong downslope prevailing winds on the exposed summit throughout the fall and winter months may limit seed dispersal. There were differences between curves at the Alaska Range and Brooks Range sites, with respect to both shape (b1) and magnitude (b0) (Table 3-3). The Alaska Range sites deposited significantly higher seed densities over greater distances compared to the Brooks Range site (Figure 3-10).

The amount of seed produced by the treeline sites is small relative to production records for upland sites in interior Alaska (Zasada and Gregory 1969, Zasada et al. 1978, Densmore 1980, Coates et al. 1994). These observations suggest a very limited effective dispersal distance for white spruce at both elevational and latitudinal treeline.

The dispersal curves for the upland site at BCEF also exhibited considerable variability between individual transects and between transects on the leeward and windward sides of the stand. The dispersal curves suggest considerable influence by both wind (Figure 3-7) and seed source orientation and shape (Figure 3-6). This apparent relationship warrants further investigation employing a greater sampling intensity. Such information has important management implications; suggesting that information on the direction of seed dispersing winds could be utilized to assist in orienting seed sources to maximize seed rain into a clearing and the associated natural regeneration potential (Youngblood and Max 1992).

By analyzing seed dispersal densities at a given distance, expressed as the percent seed per unit area of within stand seedfall density, differences in stand specific seed production are removed and general comparisons between transects, sites and regions can be made. Figure 3-11 illustrates the difference in "effective" dispersal capabilities of the BCEF transects. We can characterize the "effective" dispersal capabilities of individual transects by organizing them into groups, according to a 25 percent dispersal threshold (i.e. the maximum distance at which $\geq$ 25 percent of within stand seedfall is deposited). The two transects at either end of the long axis of the source stand exhibit very ineffective dispersal capabilities. The transects oriented with the wind revealed very effective dispersal capabilities, with a maximum dispersal distance of at least 100 m from the stand edge. These results suggest that seed source orientation, with respect to prevailing winds, may be an important control upon the regenerative capabilities of a harvested site.

A comparison of "effective" dispersal capability between sites showed significant differences (Figure 3-12). The most "effective" transect for each treeline site was compared to the "effectiveness" of the BCEF leeward and windward regression curves. The BR-3A-96, DP-2C-96, and BCEF leeward curves exhibited stronger "effective" dispersal capabilities than either the BCEF windward or DP-1A-96 curves. The more "effective" curves reached a maximum threshold distance of $\geq$ 100 m versus only 50 m for the "ineffective" curves. These results suggest that the two

"effective" treeline sites may have a significant effect upon seed deposition and seedling establishment trends at higher within stand production levels.

White spruce seed production and viability

Total within stand seed production between the treeline sites and upland site exhibited differences, as reported in the literature (Zasada and Gregory 1969, Zasada et al. 1978, 1992, Viereck 1979). Seed production was both variable between sites and between years for a given site (Table 3-2). For the 1996 seed crop, three times more seed was produced at the BCEF upland site than the average of the treeline sites. It should be noted that the 1996 seed crop at BCEF ranks 11th for white spruce production levels over the past 40 years in the Fairbanks area. The Brooks Range sites showed similar production levels to those measured in the same area by Densmore (1980).

Seed viability for all regions was low. The 1996 seed crop at BCEF had a relatively low average viability of 15 percent. This corresponds to the relatively low density of within stand seedfall. In general, the larger the white spruce seed crop the higher the viability of the seed (Alden 1985, Zasada et al. 1992, Farmer 1997). The difference between fall and spring seed collections suggests that seeds that fall during the winter, after initial snow cover, may have a lower viability than fall dispersed seed (Figure 3-9). Their were no clear trends within the distance intervals. This suggests

that the argument of decreasing viability with increasing dispersal distance, suggesting underdeveloped seeds may be carried further by wind, may not be valid.

Implications of seed production and dispersal upon natural regeneration patterns

The spatial and temporal distribution of white spruce seedlings on the landscape are directly influenced by the production and dispersal of seed. All other factors removed, seed must be produced and dispersed for there to be any chance of new seedlings becoming established. It is these processes, production and dispersal, that the land manager has the least influence upon with regards to natural regeneration (Zasada 1995). A better understanding of these processes and their interactions will improve the ability to manage for natural regeneration. This information is of particular use for modeling early white spruce regeneration patterns in interior Alaska.

Development of a generalized interior Alaska white spruce dispersal curve would allow for the simulation of seed dispersal patterns upon the landscape. Synthesizing dispersal and production information provides the ability to investigate actual seed availability (i.e. seeds/unit area) associated with a specific seed crop for seedbeds at various distances from the stand edge. Applying information on seed:seedling ratios and seedbed characteristics would provide the ability to simulate general seedling establishment patterns (Dobbs 1976, Zasada et al. 1992, Coates et al. 1994).

It is important to note that many other factors are involved in the successful establishment of seedlings upon the landscape. The actual viability of the seed dispersed and the effects of competing vegetation also play a major role in the success of natural regeneration. Although many factors would not be explicitly represented, such a model could provide valuable information on potential natural regeneration patterns of white spruce in interior Alaska.

Summary

The production and dispersal of white spruce seed in interior Alaska varies across the landscape. The episodic nature of spruce production and limited dispersal ability make it difficult to predict potential regeneration patterns. Natural regeneration of white spruce seedlings across the landscape of interior Alaska is dependent upon the availability of seed, which varies both temporally and spatially. This variability includes temporal issues of seed production that are influenced by climatic and tree physiological factors. Spatial variability is influenced by the shape and size of the seed source, production level, topographic position, and wind. This variability has important implications on the type of harvest, seed source layout, and seedbed treatment employed by the land manager.

Information on the production and dispersal of seed can assist in maximizing the probability of successful natural regeneration of white spruce. However, further investigation is needed to provide accurate descriptions of white spruce seed dispersal

across the landscape. Developing the ability to predict future seed production levels and dispersal patterns would greatly improve the ability to accurately simulate the natural regeneration potential of a particular stand, watershed, or landscape.

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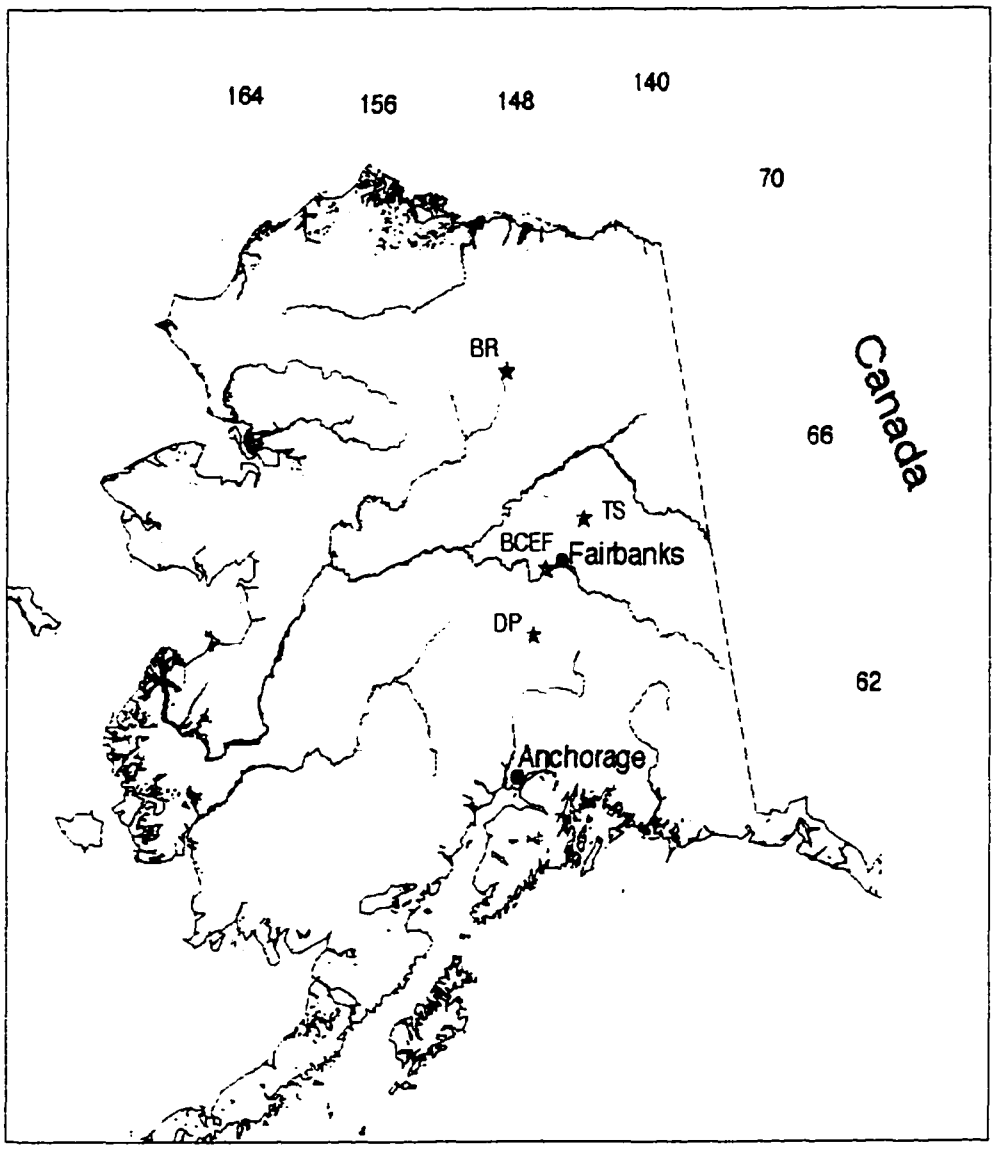

Figure 3-1. Location of seed dispersal sites. Brooks Range latitudinal treeline sites (BR), Alaska Range (DP) and White Mountains (TS) elevational treeline sites, and Bonanza Creek Experimental Forest (BCEF) upland site.

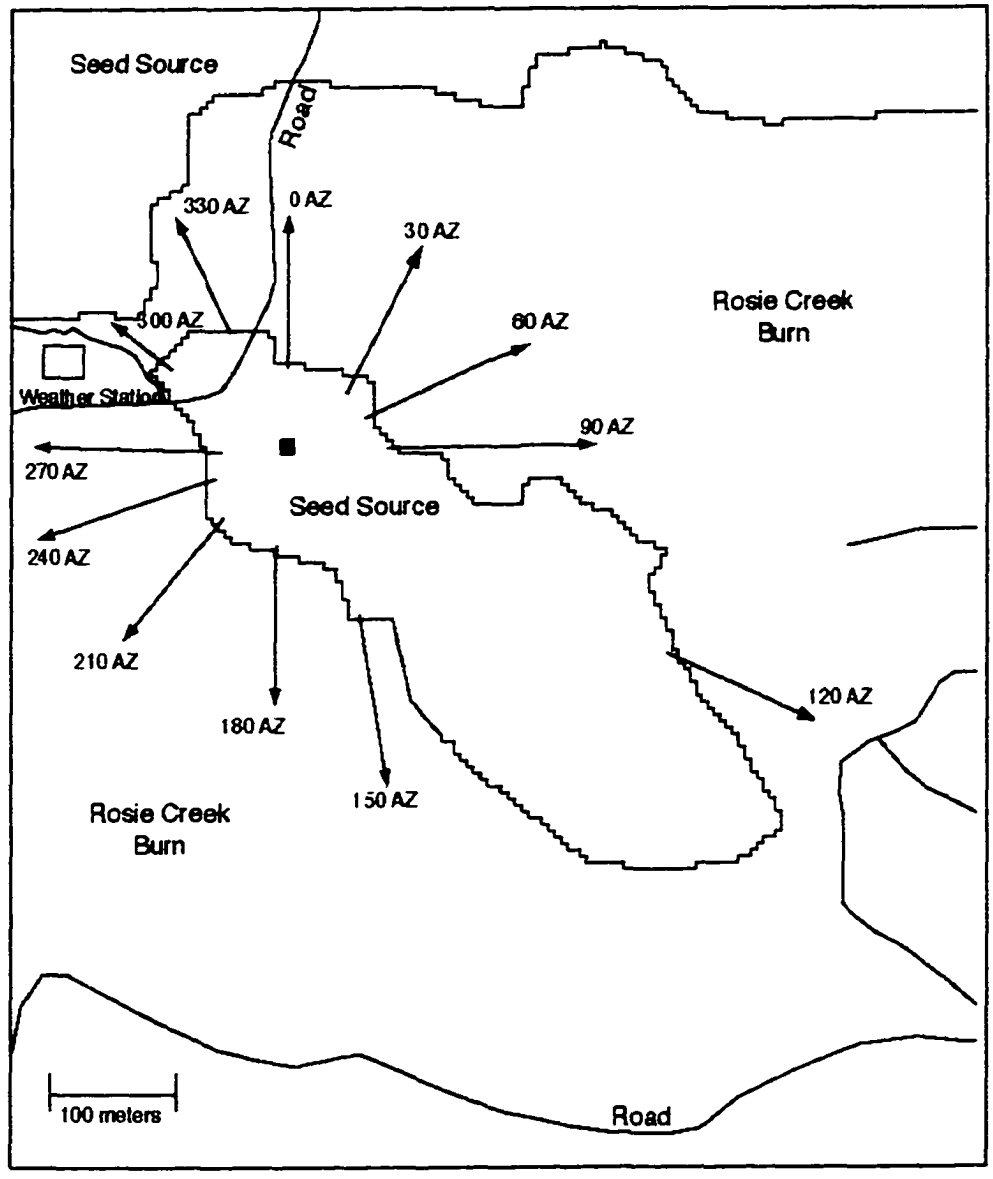

Figure 3-2. Bonanza Creek Experimental Forest (BCEF) study site, showing layout of individual transects and location of the LTER upland weather station.

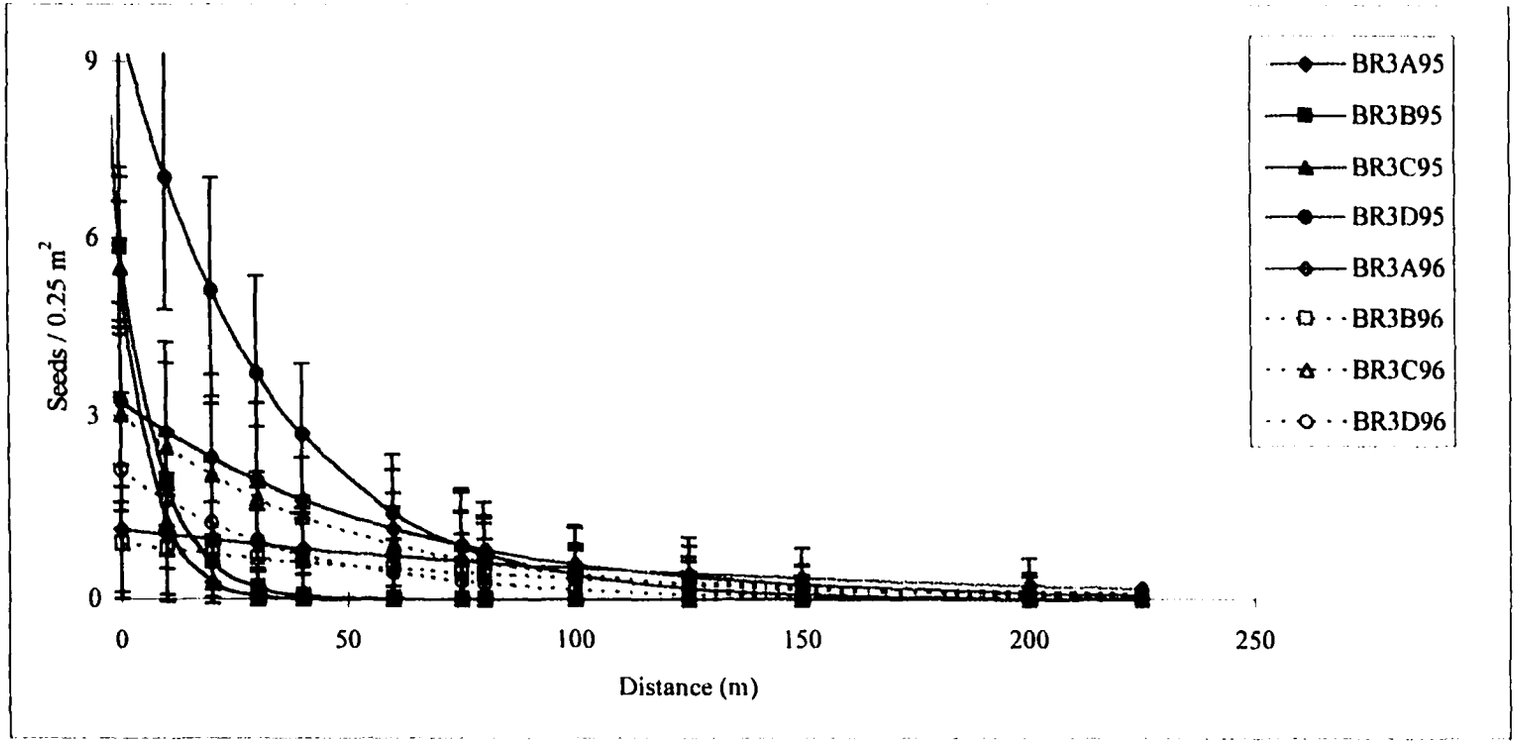

Figure 3-3. White spruce seed dispersal regression curves for individual transects at the Brooks Range (BR-3) site. Solid lines (—) represent 1995 seedfall and dotted lines (----) represent 1996 seedfall. Regression line colors represent curves with similar slope. Error bars represent a 95 percent confidence interval for the asymptotic standard error of the slope coefficient (b_1). The seed trap sample size for each transect was 10 (n = 10).

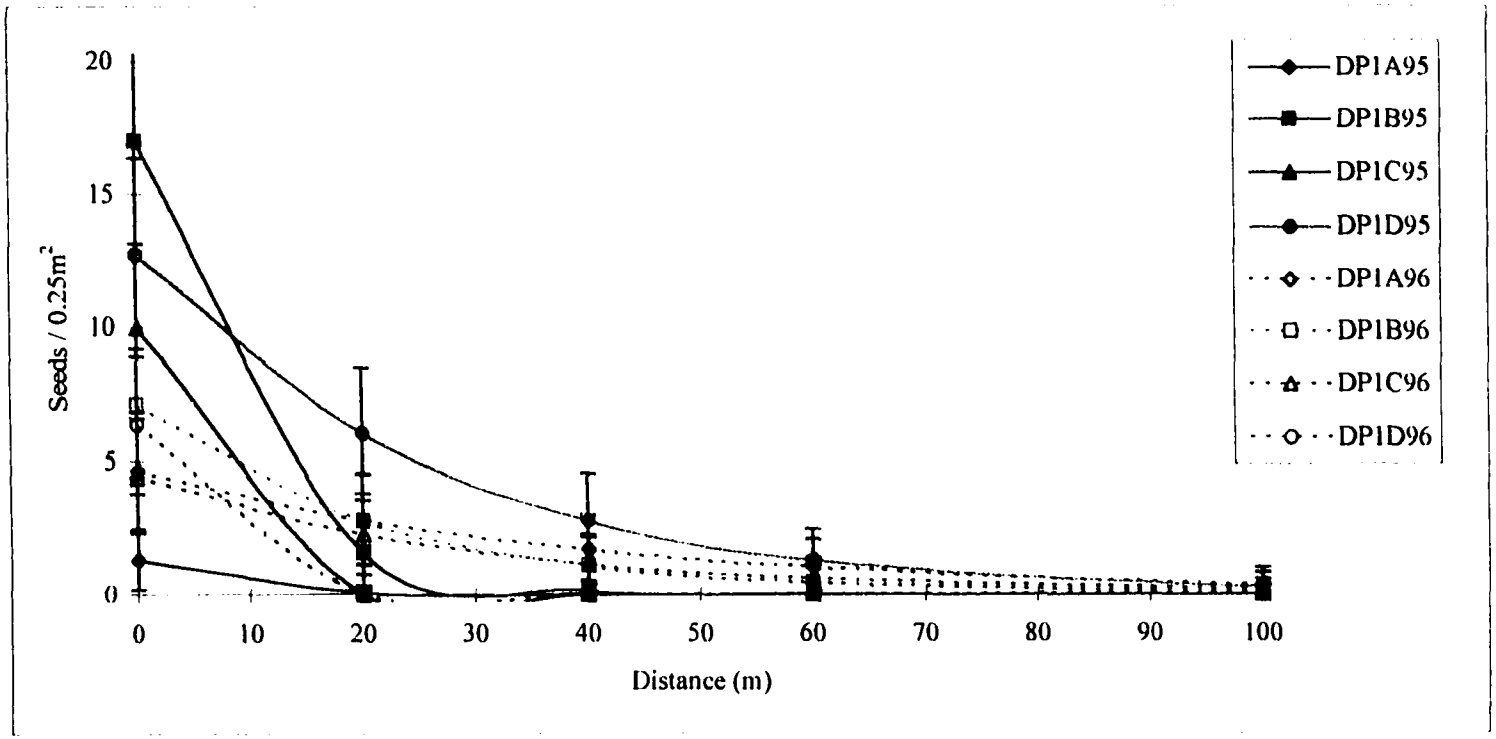

Figure 3-4. White spruce seed dispersal regression curves for individual transects at the Denali National Park (DP-1) site. Solid lines (—) represent 1995 seedfall and dotted lines (----) represent 1996 seedfall. Regression line colors represent curves with similar slope. Error bars represent a 95 percent confidence interval for the asymptotic standard error of the slope coefficient (b_1). The seed trap sample size for each transect was 10 (n = 10).

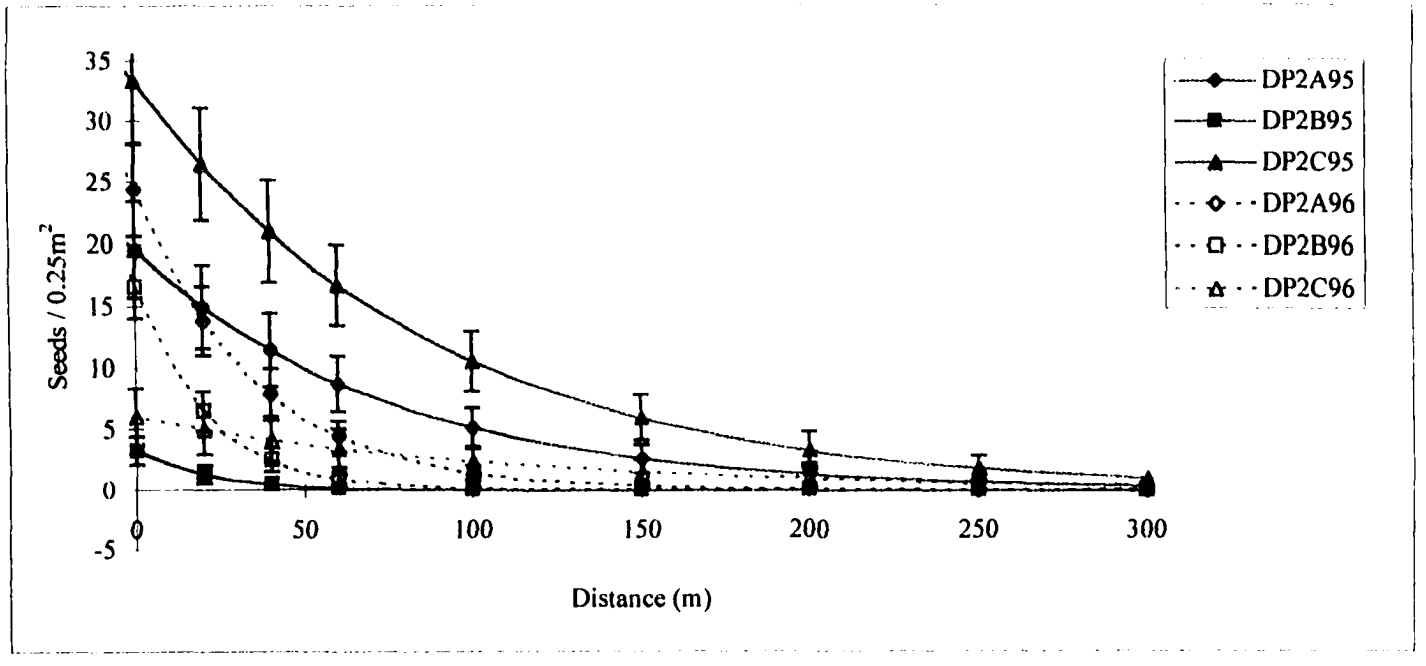

Figure 3-5. White spruce seed dispersal regression curves for individual transects at the Denali National Park (DP-2) site. Solid lines (—) represent 1995 seedfall and dotted lines (----) represent 1996 seedfall. Regression line colors represent curves with similar slope. Error bars represent a 95 percent confidence interval for the asymptotic standard error of the slope coefficient (b_1). The seed trap sample size for each transect was 10 (n = 10).

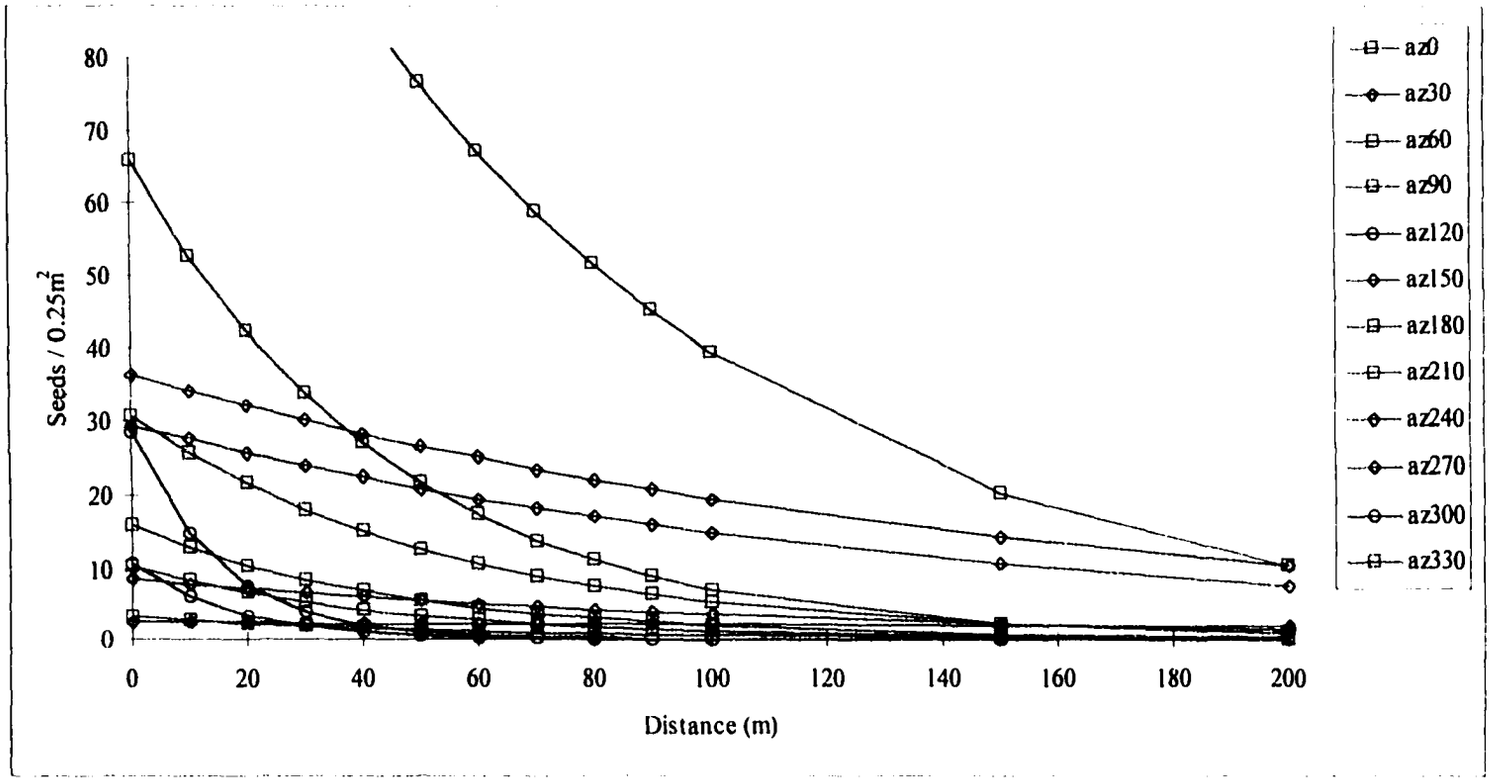

Figure 3-6. White spruce 1996 seed dispersal regression curves for individual transects at the Bonanza Creek Experimental Forest (BCEF) site. Regression line colors represent curves with similar slope. The seed trap sample size for each transect was 14 (n = 14).

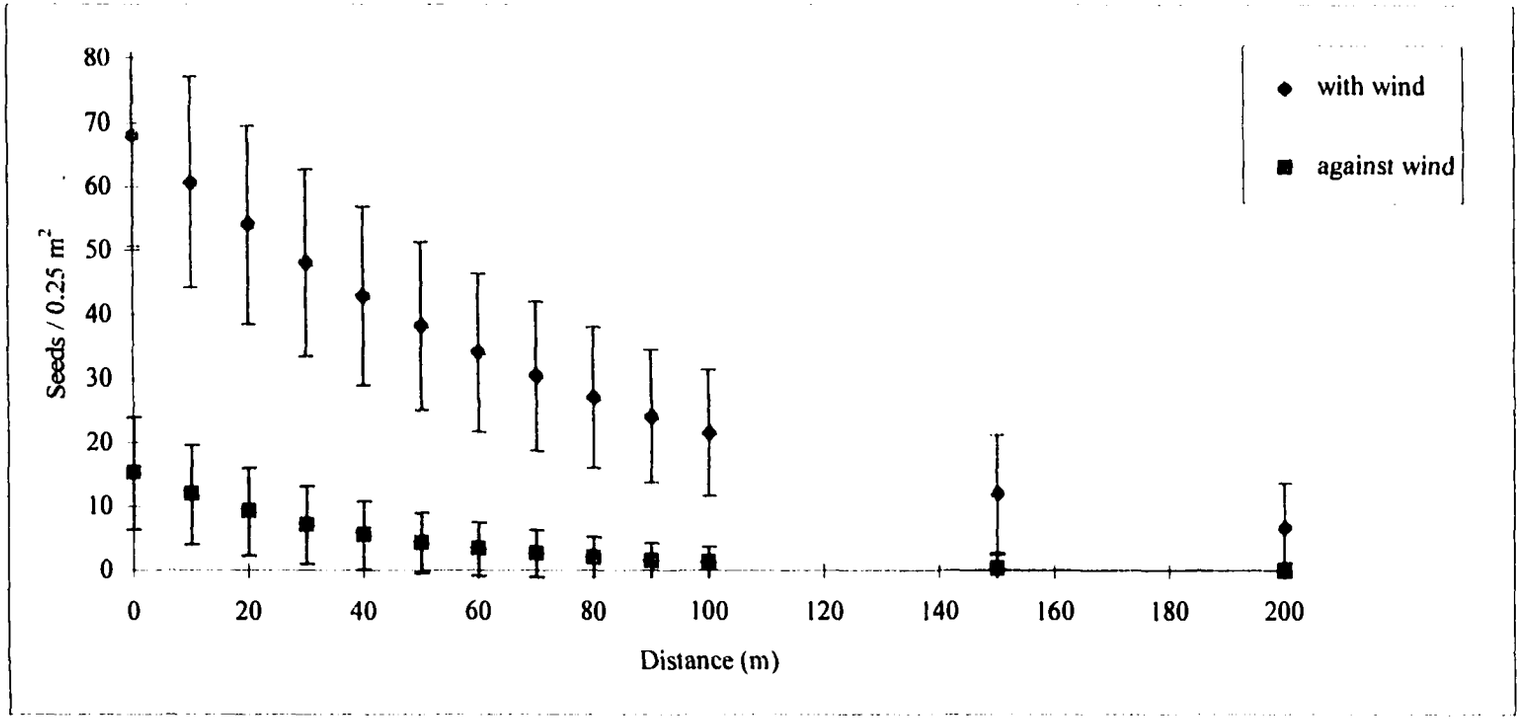

Figure 3-7. Comparison of leeward and windward white spruce seed dispersal transects at the Bonanza Creek (BCEF) site. The green line represents the leeward transects (AZ 180, 210, 240, 270) and the red line represents the windward transects (AZ 0, 30, 60, 90, 120, 150, 300, 330). Error bars represent a 95 percent confidence interval for the asymptotic standard error of the slope coefficient (b_1).

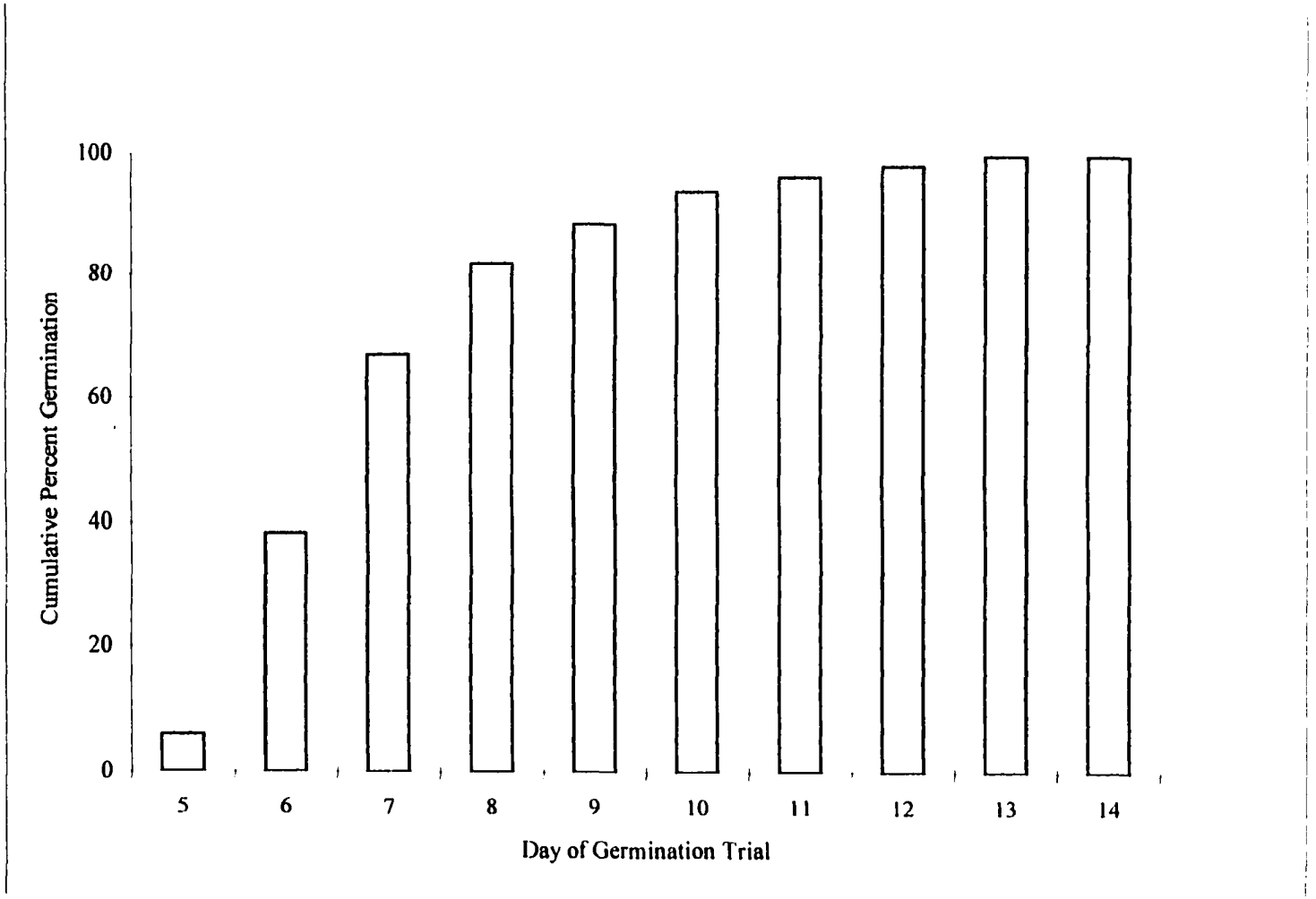

Figure 3-8. Time series of cumulative percent germinated seed from germination trials. The total sample size was 1500 seeds (n = 1500).

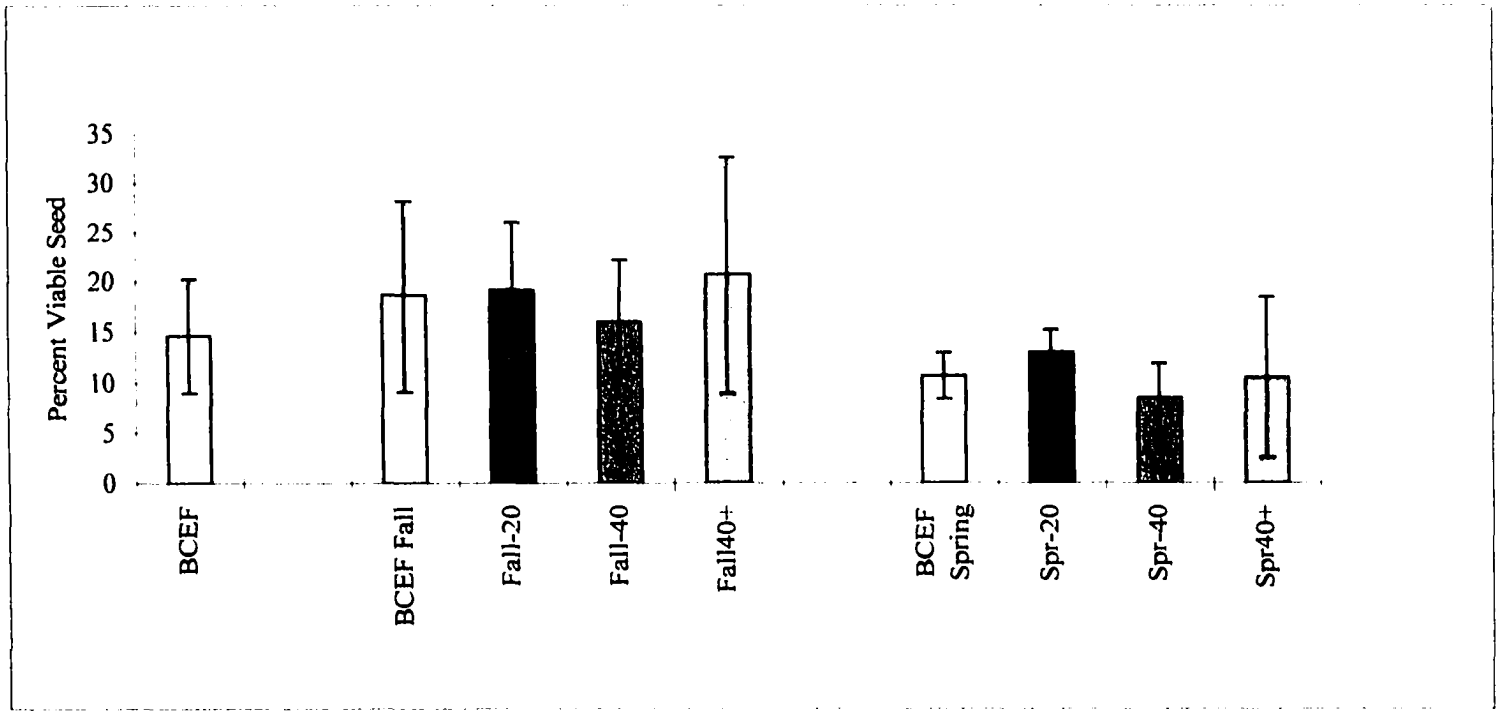

Figure 3-9. Comparison of seed viability for the 1996 seed crop at the Bonanza Creek (BCEF) site. The figure compares total average viability (white bars), viability of seed dispersed less than 20 m from the stand edge (dark bars), seed dispersed between 20 and 40 m (gray bars), and seed dispersed greater than 40 m (light gray bars) for both fall and spring seed collections. Each germination sample had 25 seeds and was replicated 4 times (n = 600).

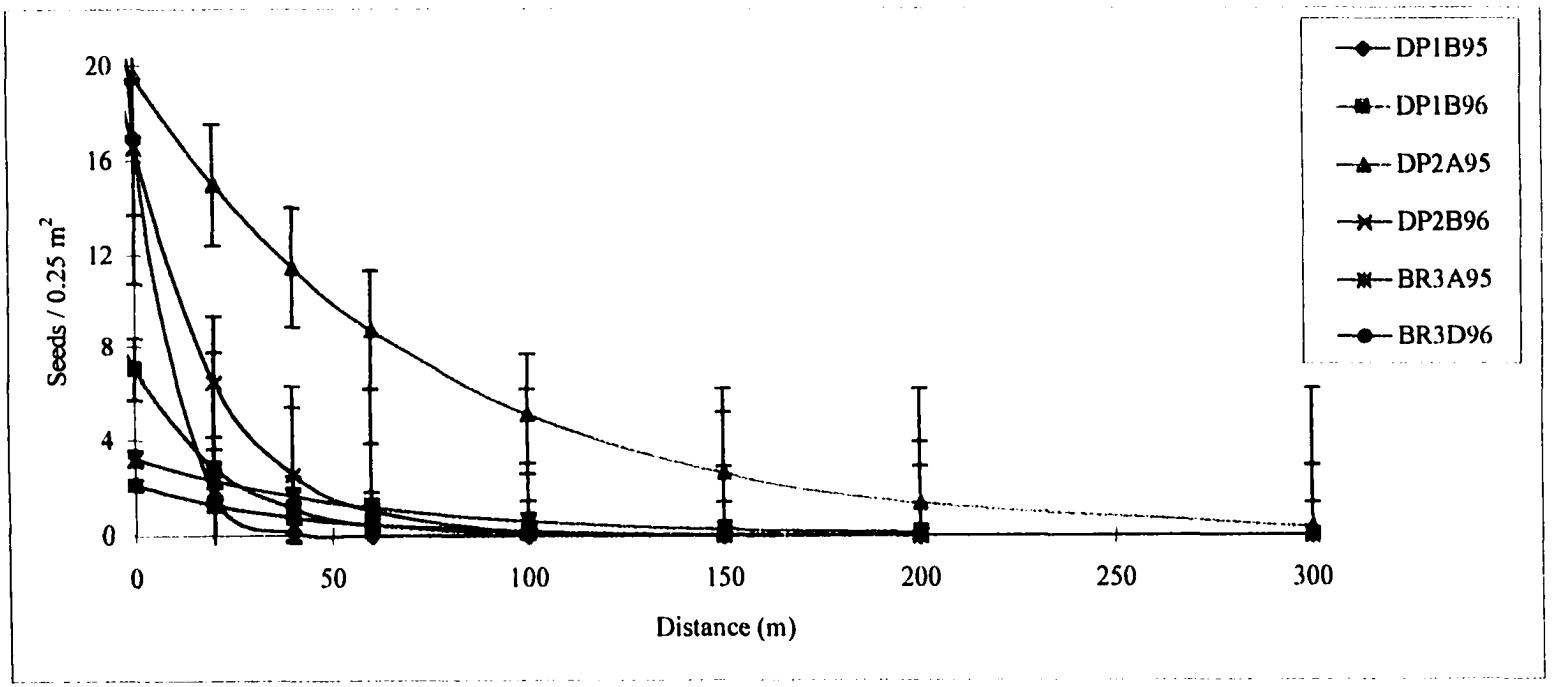

Figure 3-10. Comparison of white spruce seed dispersal curves from latitudinal (Brooks Range) and elevational (Alaska Range) treeline sites. Regression line colors represent curves with similar slope. Error bars represent a 95 percent confidence interval for the asymptotic standard error of the slope coefficient (b_1). The seed trap sample size for each transect was 10 (n = 10).

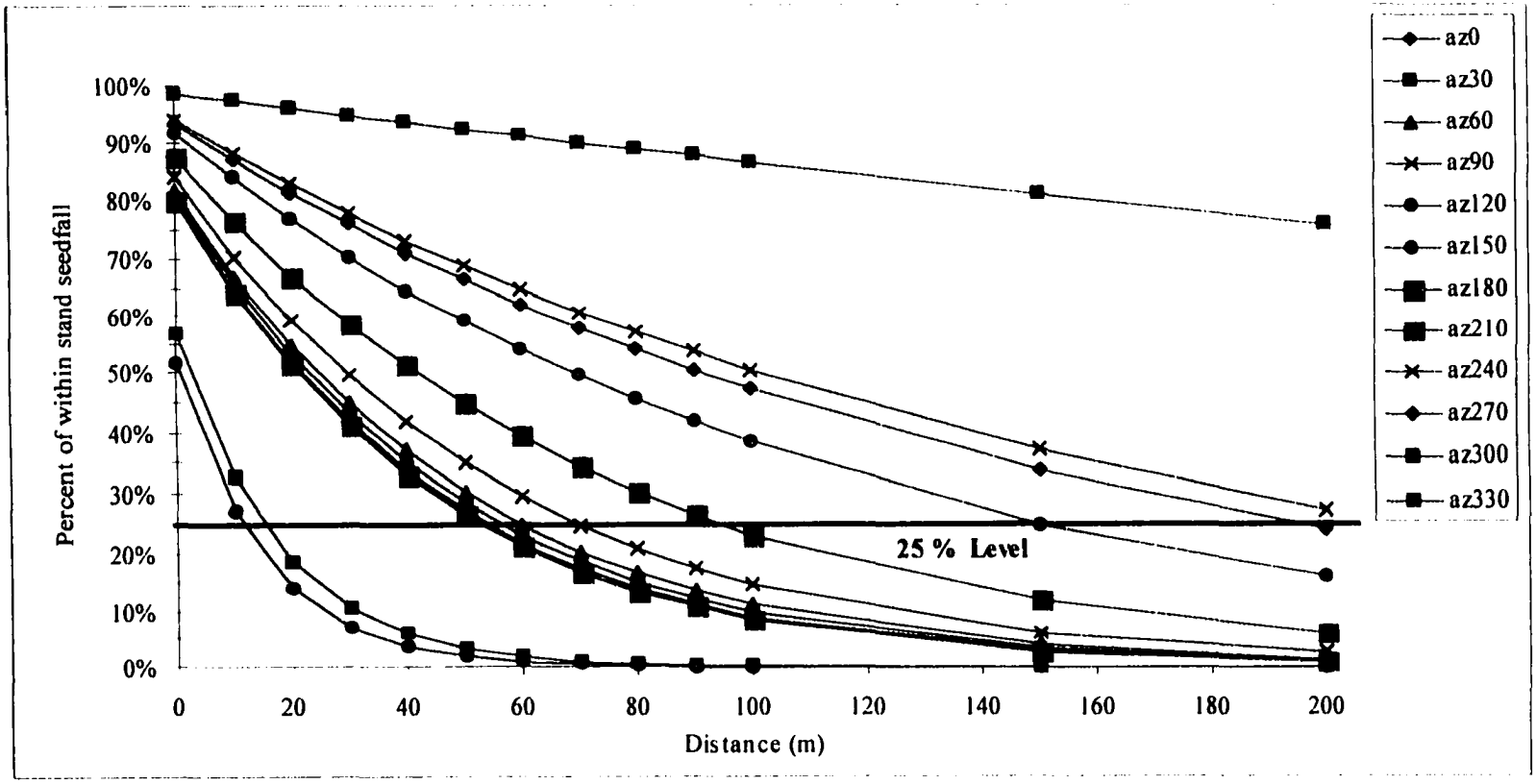

Figure 3-11. Comparison of white spruce seed dispersal efficiency at the Bonanza Creek (BCEF) site. Dispersal efficiency is represented as the percent of within stand seedfall. Regression line colors represent curves with similar slope. The 25 percent threshold line represents the distance at which 25 percent or more of within stand seedfall densities are dispersed. The seed trap sample size for each transect was 14 (n = 14).

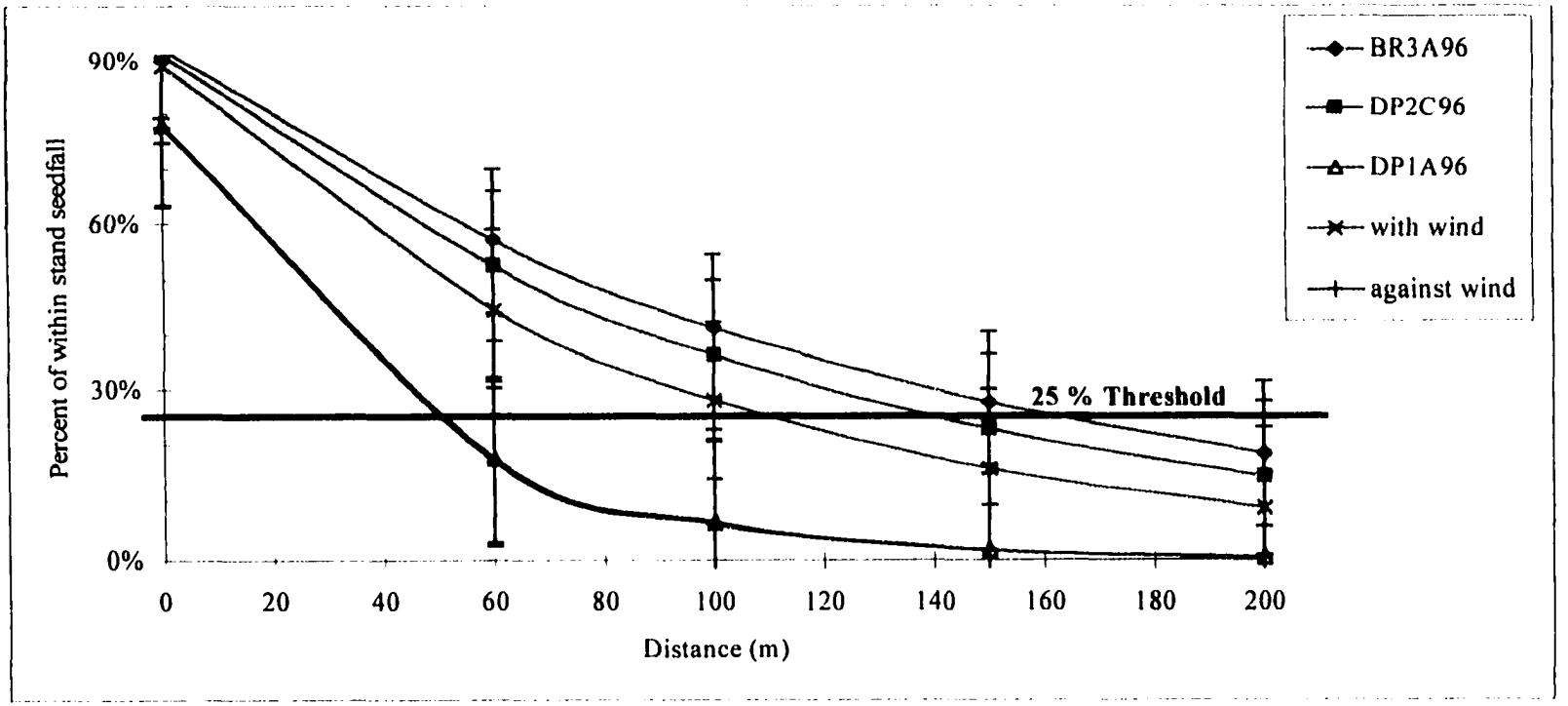

Figure 3-12. Comparison of efficiency curves across regions. Comparison of white spruce seed dispersal efficiency across interior Alaska. Dispersal efficiency is represented as the percent of within stand seedfall. The 25 percent threshold line represents the distance at which 25 percent or more of within stand seedfall densities are dispersed.

Table 3-1. Stand characteristics for individual study sites. Source stands represent the Alaska Range sites (DP-1 and DP-2), White Mountains site (TS), Brooks Range sites (BR-1, BR-2, and BR-3), and the Bonanza Creek Experimental Forest (BCEF). Stand characteristics were measured using standard point sampling techniques. Each stand had 10 point samples (n = 10), using a BAF 10 wedge prism.

Source Stand	BA (m^2/ha)	Ave. DBH (cm)	Ave. Ht. (m)	Trees/ha	Ave. Age at DBH
DP-1	12.85	27.14	7.48	263.65	135
DP-2	8.72	29.21	8.55	205.34	144
TS	12.63	25.55	8.20	310.35	148
BR-1	13.26	12.12	6.68	719.55	105
BR-2	12.05	16.9	7.68	485.05	110
BR-3	12.05	13.67	7.37	588.09	137
BCEF (spruce)	23.53	32.08	19.09	251.54	180
(birch)	13.2	27.65	14.88	216.95	-

Table 3-2. White spruce seed production and dispersal observations for individual study sites. Source stands represent the Alaska Range sites (DP-1 and DP-2), White Mountains site (TS), Brooks Range sites (BR-1, BR-2, and BR-3), and the Bonanza Creek Experimental Forest (BCEF). Sample size was 40 seed traps for each treeline study site (n = 40) and 168 seed traps at BCEF (n = 163).

Seed Year	Seed Source	Average Within Stand Seedfall (seeds/m^2)	Average Seedfall at 40 m	Average % of Within Stand	Average Seedfall at 100 m	Average % of Within Stand	Maximum Dispersal
1995	DP-1	60.0 ± (33.9)	7.0 ± (8.2)	11.7	3.0 ± (2.0)	5.0	300
	DP-2	46.0 ± (36.8)	16.0 ± (18.3)	34.8	12.0 ± (10.6)	26.1	250
	BR-1	12.0 ± (5.7)	4.0 ± (0.0)	33.3	0.0 ± (0.0)	0.0	40
	BR-2	12.0 ± (11.3)	0.0 ± (0.0)	0.0	0.0 ± (0.0)	0.0	20
	BR-3	54.0 ± (59.4)	1.0 ± (2.0)	1.9	1.0 ± (2.0)	1.9	100
	TS	9.0 ± (7.6)	*	*	*	*	*
	BCEF	0.0 ± (0.0)	*	*	*	*	*
1996	DP-1	28.0 ± (17.0)	6.0 ± (5.2)	21.4	1.0 ± (2.0)	3.6	200
	DP-2	90.0 ± (25.5)	14.7 ± (14.1)	16.3	8.0 ± (8.0)	8.9	200
	BR-1	2.0 ± (2.8)	0.0 ± (0.0)	0.0	0.0 ± (0.0)	0.0	10
	BR-2	2.0 ± (2.8)	0.0 ± (0.0)	0.0	0.0 ± (0.0)	0.0	10
	BR-3	12.0 ± (5.7)	3.0 ± (3.8)	25.0	0.0 ± (0.0)	0.0	125
	TS	75.3 ± (30.6)	*	*	*	*	20
	BCEF	139.4 ± (100.3)	70.3 ± (122.5)	50.4	28.0 ± (30.2)	20.1	200

* indicates no observation

Table 3-3. Treeline regression equation coefficients, standard errors, and 95 percent confidence intervals. Source stands represent the Alaska Range sites (DP-1 and DP-2), and Brooks Range sites (BR-1, BR-2, and BR-3). The sample size was 10 for each transect (n = 10). Seed dispersal equation is: $Y = b_0 e^{-b1X}$.

Transects	b0	std. Error[1]	95 % CI[2]	b1	std. Error[1]	95 % CI[2]
DP1A 1995	1.36	0.95	0 - 3.26	0.1416	0.0238	0.094 - 0.2118
DP1B 1995	16.97	1.84	13.29 - 20.65	0.1185	0.0753	0 - 0.0753
DP1C 1995	10	n.a.	n.a.	1.7668	n.a.	n.a.
DP1D 1995	12.77	0.93	10.91 - 14.63	0.0376	0.0065	0.0246 - 0.0557
DP1A 1996	4.66	0.92	2.82 - 6.5	0.0248	0.0109	0.003 - 0.0169
DP1B 1996	7.08	1.18	4.72 - 9.44	0.0458	0.0152	0.0154 - 0.046
DP1C 1996	4.47	1.02	2.43 - 6.51	0.033	0.0136	0.0058 - 0.0252
DP1D 1996	6.36	14.35	0 - 35.06	0.2556	0.2248	0 - 0.02248
DP2A 1995	19.62	5.89	7.84 - 31.4	0.0134	0.0092	0 - 0.0318
DP2B 1995	3.33	0.68	1.97 - 4.69	0.0456	0.0198	0.006 - 0.0852
DP2C 1995	33.39	22.04	0 - 77.47	0.0115	0.0155	0 - 0.0425
DP2A 1996	24.4	7.88	8.64 - 40.16	0.0282	0.0197	0 - 0.0676
DP2B 1996	16.59	3.37	9.85 - 23.33	0.0468	0.0201	0.0066 - 0.087
DP2C 1996	6.08	1.04	4 - 8.16	0.0092	0.0042	0.0008 - 0.0176
BR3A 1995	3.25	0.48	2.29 - 4.21	0.0172	0.006	0.0052 - 0.0292
BR3B 1995	5.86	0.64	4.58 - 7.14	0.1132	0.0368	0.0396 - 0.1868
BR3C 1995	5.5	0.51	4.48 - 6.52	0.1471	0.0095	0.1281 - 0.1661
BR3D 1995	9.73	4.98	0 - 19.69	0.0321	0.0261	0 - 0.0843
BR3A 1996	1.16	0.44	0.28 - 2.04	0.008	0.0076	0 - 0.0232
BR3B 1996	0.93	0.62	0 - 2.17	0.0102	0.0126	0 - 0.0354
BR3C 1996	3.03	1.17	0.69 - 5.37	0.0201	0.0163	0 - 0.0527
BR3D 1996	2.12	0.62	0.88 - 3.36	0.0262	0.0124	0.0014 - 0.051

[1] Asymptotic standard error.
[2] Coefficient 95 percent confidence interval.

Table 3-4. Bonanza Creek (BCEF) regression equation coefficients, standard errors, and 95 percent confidence intervals

The sample size was 14 for each transect (n = 14). Seed dispersal equation is : $Y = b_0 e^{-b1X}$

Transect	b0	std. Error[1]	95 % CI[2]	b1	std. Error[1]	95 % CI[2]
0 AV	15.99	2.07	11.85 - 20.13	0.0209	0.0074	0.0061 - 0.0357
30 AV	2.48	0.54	1.4 - 3.56	0.0013	0.0026	0.0 - 0.0065
60 AV	3.47	0.42	2.63 - 4.31	0.0199	0.0052	0.0095 - 0.0303
90 AV	30.57	11.01	8.55 - 52.59	0.0174	0.0108	0.0 - 0.039
120 AV	28.59	3.68	21.23 - 35.95	0.0655	0.0130	0.0395 - 0.0915
150 AV	8.6	3.2	2.2 - 15.0	0.0087	0.0088	0.0 - 0.0263
180 AV	65.93	4.32	57.29 - 74.57	0.0222	0.0029	0.0164 - 0.028
210 AV	149.12	13.94	121.24 - 177.0	0.0133	0.0024	0.0085 - 0.0181
240 AV	36.24	2.47	31.3 - 41.18	0.0062	0.0013	0.0036 - 0.0088
270 AV	29.41	4.44	20.53 - 38.29	0.0068	0.0026	0.0016 - 0.012
300 AV	10.64	1.65	7.34 - 13.94	0.056	0.0161	0.0238 - 0.0882
330 AV	10.37	1.08	8.21 - 12.53	0.0218	0.0039	0.014 - 0.0296

[1] Asymptotic standard error

[2] Coefficient 95 percent confidence interval

CHAPTER 4 - A GEOGRAPHIC MODEL OF LANDSCAPE-LEVEL EARLY POST-DISTURBANCE SEEDLING ESTABLISHMENT PATTERNS IN INTERIOR ALASKA

Introduction

Ecosystem sustainability is the major objective directing current natural resource management. Ecosystem-level management involves managing at a spatial scale of square kilometers, a scale unfamiliar to traditional forest management that has focused on stand-level dynamics at spatial scales of 10's of hectares. Geographic models of forest establishment dynamics accommodate this broader landscape-level management scale and provide information critical to ecosystem management at landscape- and regional-levels.

A geographic information system (GIS) provides an explicitly defined landscape. Spatially explicit processes and driving variables that influence vegetation patterns upon the landscape can be represented. For example, the production and dispersal of seed across the landscape and the seedbed conditions encountered by the seed directly affect subsequent establishment patterns. These patterns reflect the landscape, representing the variability of the various biotic and abiotic factors influencing the establishment process. Harper (1977) describes these factors as an "environmental sieve" that acts upon seedling establishment. These factors vary across

the landscape, with a unique combination present at any one time and point upon the landscape.

Traditional forest establishment models follow the gap-type modeling paradigm of JABOWA (Botkin et al. 1972a, 1972b) and its offspring FORET (Shugart and West 1977), LINKAGES (Pastor and Post 1985), and the spatially explicit model, SORTIE (Pacala et al. 1993, Tester et al. 1997). These models work at the stand-level and, with the exception of SORTIE, are not spatially explicit. The process of early seedling establishment (regeneration) is, for the most part, represented by the model assumptions. These broad assumptions apply to both the processes and driving variables behind establishment and to the landscape itself. For example, the production and availability of seed is assumed to be constant and the environment is assumed to be conducive to the establishment of seedlings (Botkin et al. 1972a, 1972b, Shugart and West 1977). Such assumptions limit realistic representation of landscape variation and its influence on driving processes and variables.

The landscape mosaic of interior Alaska results from disturbance patterns, both temporal and spatial, and the biotic and abiotic factors acting upon the landscape. Fire regularly resets the successional clock within the uplands (Van Cleve et al. 1991). These uplands are a mixture of productive white spruce stands, hardwoods, mixed stands, and relatively unproductive black spruce stands. Forest management in interior Alaska has focused on the more productive stands, directing a majority of management actions toward white spruce systems.

White spruce is scattered throughout the more productive southerly aspect uplands and along the river floodplains of interior Alaska. The mosaic pattern of white spruce reflect its close relationship to disturbance and position within the successional trajectories of the interior Alaska boreal forest. The persistence of white spruce in the landscape is strongly tied to the interactions of disturbance and the episodic nature of white spruce seed production and dispersal (Zasada et. al 1992).

Current harvesting and subsequent regeneration practices rely principally upon seedling planting. In addition to the economic impacts, such a management strategy reduces genetic diversity and runs the risk of decreasing the long-term ability of white spruce systems to persist naturally across the landscape (Zasada 1995, Farmer 1997). These practices have been implemented, in part due to the lack of information and understanding of the driving processes and factors behind early white spruce establishment.

The objective of this study was to develop a geographic model of early post-disturbance establishment patterns of upland white spruce ecosystems in interior Alaska. The model provides a tool for investigating the effects of specific management scenarios and silvicultural schemes upon early establishment patterns. Model results provide information on important processes and factors that influence white spruce establishment patterns and identify critical information gaps in our knowledge base.

The Model

Background

The Alaskan Boreal Forest Establishment Model (ABFEM) is a geographic model of forest tree seedling establishment within burnt upland white spruce ecosystems of interior Alaska. The model simulates the production of seed (white spruce and paper birch), the reproductive potential of the landscape including both the seed (white spruce and paper birch wind dispersed seed) and vegetative bud bank (paper birch basal sprouts and aspen root suckers), and the early establishment of seedlings and vegetative stems (white spruce, paper birch, and aspen) in relation to climate, topography, disturbance effects, competing vegetation, and forest floor depth, which are implicitly represented through the characterization of the seedbed and the use of a dynamic seed:seedling index. The index represents the number of viable seed needed to produce one established seedling given the time since disturbance (i.e. fire) and the specific post-fire seedbed conditions. Vegetative regeneration is implicitly represented by the availability of a bud bank (i.e. pre-disturbance vegetation) and the effects of disturbance upon the forest floor.

An established seedling, as defined in the model, is a 5 yr old, free to grow seedling (Eis 1967). When viewed as a cohort, the majority of seedling mortality (i.e. 90 percent) has occurred (Zasada et. al. 1978) by this time. White spruce and paper birch seedlings are both characterized by heavy mortality the first two years, with little mortality occurring after 3 to 5 years (Eis 1965, Zasada et. al. 1978, 1992).

The model simulates the hypothesized controls and factors that drive upland white spruce establishment patterns. This approach was followed for two reasons. First, there is a limited understanding of the complexities of natural regeneration dynamics within interior Alaska, supported by the lack of empirical data available for model development and validation. Second, to provide the land manager with useful information which can be used to explore various management scenarios, the model should capture only the most essential components of the ecosystem. Complex models require a high level of detail, the required data is both expensive and time consuming to collect at the landscape-level. Furthermore, the complexity makes it difficult to understand what causes a particular response by the system. Modeling only the most essential controls (i.e. seed production and dispersal, seedbed conditions, and seedling survival and establishment) and relationships (i.e. temporal and spatial pattern of disturbance, seedbed receptivity, and seed availability), we can explore the general response of the system and how one may create or avoid specific responses to meet management objectives.

Methods

Model Overview → f(seed availability, seed rain, seedbed receptivity, mortality)

ABFEM was created within the GRID environment of ARC/INFO (ESRI 1994). Each routine runs entirely within ARC/INFO utilizing a complex set of Arc Macro Language routines (AML's). The model runs on an annual timestep and at a

spatial scale of 100 m^2 (10 m x 10 m cells). Routines utilize grids and scalars; cell and scalar values represent parameter (input and output) values. ABFEM simulates the production and dispersal of seed, disturbance effects upon the seedbed, and early establishment of seedlings and vegetative stock. The model outputs the number of white spruce and paper birch seedlings, and the presence of aspen and paper birch vegetative stems established following disturbance in upland white spruce ecosystems of interior Alaska. Additional output provides seed production trends, seed dispersal patterns, disturbance patterns, and vegetative versus seed reproduction patterns across the landscape.

Empirical data used to develop and calibrate individual routines were measured in the Fairbanks area of interior Alaska over the past 4 decades. Information from the literature was used to fill certain knowledge gaps. Model validation was carried out through comparison of model predictions with the literature and observations from interior Alaska. Sensitivity analysis of individual model components identified important variable thresholds.

Seed Production → f(climate, growth reserves, predation)

The production of seed simulates the total annual viable seed produced per unit area within a given seed source. The procedure function of SEEDS:

$$Y = f(\text{previous crop, stochastic})$$

stochastically simulates annual seed production of white spruce and paper birch, incorporating the negative effects upon growth reserves resulting from the previous production event. The influence of climate and predation upon the level of seed production is represented stochastically. A simple rule represents the depletion of growth reserves following an excellent production event, resulting in the inability to produce consecutive bumper crops. A probability distribution was developed from a 40 yr record of seed production in the Fairbanks area (Figure 4-1), providing total and viable annual seed densities associated with a given cone crop rating (excellent, moderate, poor) (Zasada and Viereck 1970, Zasada and Gregory 1972, Kelly 1978, Zasada 1985, Youngblood and Max 1992).

The following assumptions apply to white spruce: (i) cone crops can be classified as poor, moderate-good, or excellent (classification relates to within stand total seedfall per square meter, where poor < 100 total seeds/m^2, moderate-good ≥ 100 and < 1000 total seeds/m^2, and excellent ≥ 1000 total seeds/m^2); (ii) the probability of a successful cone crop (i.e. either a moderate-good or excellent rating) is 0.30; (iii) similarly the probability of a successful cone crop being rated excellent is 0.40 (i.e. the overall probability of an excellent cone crop is 0.12); (iv) successive excellent cone crops do not occur (Matthews 1963, Fox et al. 1984, Zasada et al. 1992, Farmer 1997); (v) for any given cone crop rating the actual total and viable seed produced, expressed as density per unit area falling within the stand, is variable.

Using the above assumptions, a simple routine was developed to simulate the irregular production and inherent variability in white spruce cone and seed production in interior Alaska. First, a uniform random number between 0 and 1 is generated, called R_1. If R_1 is less than or equal to 0.30, the cone crop is classified successful, otherwise it is rated as a poor crop. If a successful crop is produced a second uniform random number between 0 and 1 is generated, called R_2. If R_2 is less than or equal to 0.40 (i.e. overall probability of 0.12), the cone crop is rated excellent, otherwise it is rated moderate-good. A simple rule, stating that if the previous year's rating was excellent the current year is rated poor, represents a physiological response to bumper crops (Matthews 1963, Zasada et al. 1992, Farmer 1997).

Secondly, a probability distribution of total modeled seedfall associated with each rating is created, from the means and standard deviations from a 40 yr empirical record. Total modeled seedfall density for each rating is randomly assigned from the corresponding modeled distribution. A probability distribution of percent viable seed is similarly created. The number of viable seeds produced is then calculated by multiplying the total seed and percent viable variables.

Paper birch catkin and seed production simulation follow the same technique used for white spruce. The following assumptions apply: (i) paper birch catkin crops can be classified as poor, good, or excellent (classification relates to within stand total seedfall per square meter, where poor < 3000 total seeds/m^2, moderate-good $\geq$ 3000 and < 25000 total seeds/m^2, and excellent $\geq$ 25000 total seeds/m^2); (ii) the probability

of a successful crop (i.e. either a good or excellent rating) is 0.60; (iii) similarly the probability of a successful crop being rated excellent is 0.42 (i.e. the probability of an excellent catkin crop is 0.25); (iv) successive excellent crops do not occur (Matthews 1963, Fox et al. 1984, Zasada et al. 1992, Farmer 1997); (v) for any given rating the actual total and viable seed produced, expressed as density per unit area falling within the stand, is variable.

The model was run for 40 yr and replicated 100 times. Table 4-1 compares observed and predicted white spruce seed production trends for the Fairbanks region of interior Alaska, for the period 1957-1997. The model performed well at simulating general patterns in irregular seed production and seedfall density, but could not accurately predict the past four decades from the production record. Table 4-1 also shows the sensitivity of the model to changes in the probability of successful seed production events. Predicted values for both a 10 percent increase and decrease in probability success are presented.

The routine output is the number of viable seed per unit area (100 m^2) produced within the source stand. The seed production values for white spruce and paper birch are used as input variables by the dispersal routine. The model does not simulate aspen seed production, only vegetative reproduction of aspen is simulated.

Seed Dispersal → f(source strength, wind, topography, predation)

The dispersal of seed simulates the dispersal of total annual viable seed from a given seed source(s) upon the landscape. The procedure function for DISPERSE is:

$$Y\ [\text{viable seeds}] = b_0 * \exp(b_1 * X),\quad [\text{wind}]$$

where

Y = percent viable seed dispersed at distance X of that produced within the source stand,

X = distance from the source stand in m, and

b_0 and b_1 = regression coefficients.

simulates seed rain as a function of distance from the seed source, where at a given distance the percent total viable seed dispersed, of within stand total annual seedfall, is represented. Natural predation is assumed to occur. A set of simple rules allows for the simulation of wind influence upon the seed shadow, where seeds dispersing against "seed dispersing winds" are dispersed at lower densities and shorter distances. A negative exponential regression was applied to seed dispersal data from across interior Alaska to develop appropriate dispersal algorithms for both white spruce and paper birch.

The routine allows simulation of different production levels and associated spatial patterns of dispersed viable seed, without having to develop a new regression for each production level. The Euclidean distance of each cell within the disturbed area

to the closest source cell (X) is calculated. This distance grid is input into the dispersal algorithm to create a grid of dispersal densities (Y).

A subroutine provides for the simulation of seed dispersing wind effects upon the spatial distribution of white spruce seed about its source. Wind direction is input as a range, using a lower and upper azimuth, directions outside the input range are assumed to be oriented against the wind. The direction of each cell within the disturbed area to the closest source cell is calculated and used to determine the proper dispersal equation to be applied. Separate dispersal curves were developed for white spruce seed dispersing with the wind and seed dispersing against the wind. Wind velocity is not explicitly modeled.

The procedure provides input for the establishment procedure, providing the density of seed dispersed upon the landscape. This provides a measure of "propagule strength" across the landscape.

Disturbance Effects → f(severity, topography, neighborhood effects)

Disturbance effects simulate the degree of overstory mortality and consumption of the forest floor. The procedure function for DISTURB:

$$Y = f(\text{topography, stochastic})$$

simulates the effects of disturbance (fire) upon the seedbed, which implicitly represents the "receptivity" of a given site for seed germination and seedling establishment. Burn severity is stratified (unburned, scorched, light, medium, heavy) across the landscape

stochastically. Topography (aspect) is explicitly described and mediates the severity of burning, where the level of disturbance (amount of forest floor consumed) is reduced on northerly aspects. This implicitly represents the influence of permafrost and forest floor thickness and vegetation type upon disturbance severity. Burn patterns are assumed to be heterogeneous at multiple spatial scales.

The routine produces a heterogeneous (random) burn pattern across the landscape, resulting in various degrees of forest floor consumption. A grid of random numbers is produced for the disturbed area and stratified into 1 of 5 burn severity classes (Dyrness and Norum 1983). The probability of occurrence of a specific severity class is input. Several burn patterns can be created using the initial classified disturbance grid and various focal functions (i.e. FOCALMEAN and FOCALMAJORITY) within GRID (ESRI 1994). These reclassified grids represent neighborhood influences upon individual cells. For instance, if the majority of cells around a cell (i.e. its neighborhood) are severely disturbed the likelihood of that cell also being severely disturbed is probably high. Using the function FOCALMAJORITY, we can reclassify each cell within a grid by determining the initial classification of its neighbors and then producing a reclassified grid whose cell values reflect the majority value of its neighborhood.

Establishment → f(seedbed, germination and survival, competition)

Establishment simulates the early establishment patterns of seedlings and vegetative reproduction following disturbance. Establishment success can be further defined in terms of:

- seedbed → *f(disturbance severity, topography, vegetation)*
- germination and survival → *f(seedbed, topography, mortality)*
- competition → *f(growing space, light, water, nutrients).*

An established seedling is defined in the model as a seedling that has survived 5 years and, viewed as a cohort, the majority of seedling mortality has occurred (i.e. 90 percent) by this time. The procedure function for ESTABLISH:

$$Y = f(\text{seedbed, seed:seedling index, seedling density})$$

simulates the early establishment patterns of seedlings upon the landscape created from a given seed crop and seed rain falling upon a given seedbed. The routine implicitly simulates various biotic and abiotic factors, including climate, disturbance effects, competing vegetation, and forest floor depth, which determine the germination, survival, growth, and initial establishment of a seedling. Establishment is modeled as a function of "propagule strength" and seedbed "receptivity".

A seed:seedling index calculates the number of seeds on a given site, disturbed to a given severity, at x years since the disturbance, needed to produce one 5 yr old established seedling. As time since disturbance (x) increases so does the index value. The index determines the number of viable seeds needed to produce a seedling and changes depending on the effects of the disturbance and time since disturbance (x).

The actual index value used by an individual cell is randomly drawn from a normal distribution around the mean index values, which were determined from a literature search on seed:seedling ratio studies for white spruce and paper birch (Table 4-3a,b, and 4-4). The random values result in cell to cell variability between two cells at the same distance and with the same disturbance severity classification. Topography (aspect) is explicitly described and changes the seed:seedling index, simulating topographic effects upon seedling establishment patterns (Table 4-2). For instance, more white spruce seeds will be needed to produce a seedling located on a northerly aspect than on a southerly aspect. This implicitly represents the influence of topography, climate, and vegetation upon soil properties and competitive processes.

Vegetative reproduction is simulated for both paper birch and aspen with the SPROUT subroutine. Occurrence of vegetative reproduction within an individual cell is determined by the pre-disturbance vegetation and the severity of disturbance. There is a certain probability of occurrence associated with the pre-disturbance vegetation. For example, the probability of aspen sucker sprouts is higher (P = 0.45) in a cell that was classified as mixed hardwoods than a cell that was classified as white spruce/aspen (P = 0.20) or a cell classified as black spruce (P = 0.0). The probability of occurrence is further determined by the disturbance severity experienced by that cell and reflects burn conditions conducive to suckering by aspen or sprouting by paper birch. Vegetative reproduction affects white spruce establishment success, implicitly representing competition for growing space. The occupation of a cell by aspen and/or

paper birch sprouts reduces the ability of white spruce seed germination and survival. There is a certain probability that seedling establishment may be delayed, due to the competitive effects of vegetative sprouts.

The ESTABLISH routine outputs the spatial distribution of established seedlings from seed and spatial coverage of vegetative stems, resulting from the specified seed crop, vegetative stock, and seedbed conditions encountered.

Underlying Biology

ABFEM is a simplistic representation of the very complex dynamics involved in the process of seedling establishment. Although the processes of seed production and dispersal and the subsequent germination, survival, and early growth of seedlings upon the landscape appear oversimplified, each routine and subroutine were developed from a detailed theoretical foundation representing the underlying biology of the process, species, and system involved.

The stochastic representation of seed production reflects the observed irregular seed production of boreal forest tree species (Zasada et al. 1992, Farmer 1997). The episodic nature of white spruce seed production appears to indicate a certain synchrony with climate and a physiological response to the previous years production level (Rupp et. al. 1997). The literature suggests a positive response by white spruce to warm and dry weather the summer of bud initiation, differentiation, and development (Lutz 1956, Matthews 1963, Zasada and Gregory 1969, Zasada 1971, Viereck 1973, Alden 1985,

Zasada et al. 1992, Coates et al. 1994). Furthermore, white spruce appears to respond negatively to high production levels the previous year (Matthews 1963, Zasada et al. 1992, Farmer 1997). In other words, a warm and dry summer seems to initiate the potential for a large seed crop, which may or may not be mediated by other factors such as a late frost, insects, and/or the depletion of growth reserves by the production of the previous years seed crop. Paper birch seed production is also episodic, however the interval between successful crops is shorter and more regular than white spruce (Bjorkbom et al. 1965, Bjorkbom 1971, Zasada and Gregory 1972, Godman and Mattson 1985, Perala and Alm 1990, Zasada et al. 1992). It is hypothesized that paper birch seed production is influenced by the same factors that influence white spruce seed production. However, this influence does not appear to be as rigorous as in the case of white spruce. This complexity is captured by the use of probabilities to represent the stochasticity of meteorological factors and a simple rule, which represents the effects of depleted growth reserves.

The general pattern of seed dispersal of forest trees follows the negative exponential model (Okubo and Levin 1989, Willson 1992a, Farmer 1997). The distance and density of seed dispersed is influenced by the terminal velocity of the seed, height of release, wind speed and turbulence, and species specific morphological traits related to dispersal (Augspurger and Franson 1987). These factors, along with seed production level, produce the spatial distribution of seed on the landscape defined by Janzen (1971) as the "seed shadow". This spatial distribution is represented by the

general relationship between number of seeds dispersed and distance from the seed source, which is described by the model using a negative exponential distribution.

The primary dispersal agent for paper birch and white spruce seed is wind. Reports from the literature suggest the influence of winds upon the "seed shadow" (Harris 1967, Schlesinger 1970, Janzen 1971, Sharpe and Fields 1982, Zasada and Lovig 1983, Youngblood and Max 1992, Greene and Johnson 1995, 1996). The dispersal of white spruce seed involves warm, dry, fall winds that open the cone scales allowing for release of seed (Coates et al. 1994, Zasada 1995). These seed dispersing winds are specific and are associated with a particular type of weather pattern. Furthermore, the majority of white spruce seed is dispersed in a relatively short time frame, on the order of several weeks to two months, unlike paper birch that is dispersed throughout the winter. Therefore, wind may be particularly important to the "seed shadow" of white spruce. In other words, if a certain weather pattern type with characteristic winds disperses the majority of white spruce seed over a short time period, the spatial distribution upon the landscape is hypothesized to be influenced by the direction of those winds in relation to the seed source(s). This wind influence is represented by different white spruce seed dispersal equations dictated by location to the seed source(s) and the direction of the seed dispersing wind. The effect of topography on wind speed and direction is not simulated. Wind influence upon paper birch dispersal patterns is not simulated. It is hypothesized, due to the dispersal of paper birch seed throughout the winter and secondary dispersal capabilities of seed

across the snowpack, that wind does not significantly affect the "seed shadow" of paper birch across the landscape.

The establishment process, defined here as the germination, survival, and early growth of seedlings, is implicitly represented by the use of a dynamic seed:seedling index and simulation of the effects of fire and vegetative reproduction. The seed indexes were developed from the literature for both white spruce (Table 4-3) and paper birch (Table 4-4) The dynamic seed:seedling index determines the number of viable seeds needed to produce one 5 year old established seedling and is a function of time since disturbance, the effects of fire upon the seedbed, and topography. Successful establishment of seedlings from seed is further controlled by competition and site occupation by vegetative stems of paper birch and aspen.

Fire destroys the overstory and consumes the forest floor to varying degrees. Removal of the overstory provides new seedlings with increased light, as well as changing soil moisture and temperature and altering the available nutrient pool. Consumption of the forest floor also influences soil moisture and soil temperature. Furthermore, consumption of the forest floor provides seedbed conditions required for germination and reduces seedling competition. White spruce and paper birch seed can germinate and survive on a variety of seedbed conditions, but both increase their survival rates significantly on mineral soil seedbeds (Zasada et al. 1983, Fox et al. 1984, Thomas and Wein 1985, Putnam and Zasada 1986, Walker et al. 1986, Zasada et al. 1987). Mineral soil seedbeds provide conditions that are most conducive to the

germination, survival, and establishment of paper birch and white spruce seedlings. These seedbeds are associated with increased light, soil temperatures, and nutrient pools, as well as decreased competition by herbaceous and shrub species.

The severity of fire indicates the degree to which the overstory and forest floor are altered. As severity increases so does overstory mortality and forest floor consumption. Therefore, the degree of burn severity provides a classification of seedbed characteristics that can be used to determine the receptivity of the seedbed to germination, survival, and establishment of seedlings. For instance a severely burned site will be characterized by death of the overstory and almost complete consumption of the forest floor, exactly the conditions that tend to provide the most receptive seedbed for white spruce seedling establishment. It should be noted that certain types of crown fires may have little or no effect on the forest floor, resulting in a less receptive seedbed than that characterized by a severely burned site (Heinselman 1981).

Burn pattern varies across the landscape and provides a variety of seedbed conditions, which result in seedbeds ranging from not receptive to very receptive. Fire in interior Alaska, as well as in most fire-dominated systems, is heterogeneous in nature; producing a spatially variable pattern in both areal extent and intensity/severity (Lutz 1956, Quirk and Sykes 1971, Viereck 1973, Heinselman 1981, Dyrness and Norum 1983, Zasada et al. 1983, Thomas and Wein 1985, Hobbs and Atkins 1988, Ratz 1995). This heterogeneous pattern and variability in severity is stochastically represented in the model. The ability to manipulate the probability of occurrence of a

severity class and to change the pattern of classes, within the context of neighborhoods, allows for investigation of landscape heterogeneity and pattern.

Topography is a driving ecosystem variable in the boreal forest of Alaska. Topography influences almost every aspect of the boreal forest including microclimate, vegetation patterns, and disturbance patterns (Van Cleve et al. 1991, 1996). Therefore, topography will influence the receptivity of a seedbed and potentially mediate the positive effects, within the context of white spruce seedling establishment, that fire has upon the forest floor. For instance, a severe fire on a north aspect will produce a less receptive seedbed for white spruce than that same fire on a south aspect, due to differences in factors such as soil temperature, soil moisture, and vegetative competition (Clautice 1974). The influence of topography is represented by different seed:seedling index values for northerly and southerly aspects. This reflects the specific conditions required by white spruce for successful establishment upon the landscape.

Vegetative reproduction is an important recolonization strategy used by pioneering species such as paper birch and aspen (Zasada et al. 1992). Sprouting and suckering allow for almost immediate occupation of a disturbed site and the established root system provides for efficient utilization of increased nutrient pools. Vegetative reproduction provides for the immediate post-disturbance establishment of paper birch and aspen upon the landscape, as well as functioning as a competitive pressure that decreases the ability of white spruce seeds to germinate and establish on occupied sites. The ability of a species to produce vegetative stems on a given site is a function of its

pre-disturbance occurrence and the severity of the disturbance. For example, aspen root suckering is initiated by increased soil temperatures and suckers most effectively at soil temperatures of 24^0 C (Maini and Horten 1966, Gifford 1967). A window around this optimum temperature functions as the range of temperatures at which suckering will occur, temperatures outside this window will either not initiate suckering or kill vegetative buds.

These processes and factors interact and vary across the landscape. Different combinations produce different establishment patterns. Developing the model in a manner that reflects the complex underlying biology of the system in a simplistic approach allows one to investigate how certain changes in processes and/or factors can influence the pattern of natural regeneration upon the landscape.

Caveats and Pitfalls

Although four decades of boreal forest research have been conducted in interior Alaska, we still have many unanswered questions regarding issues of early natural regeneration dynamics. From a research standpoint, the model has identified critical information gaps and serves as a tool for hypothesis development and testing.

From a functional standpoint, each model routine has major shortcomings. SEEDS accurately simulates general trends in seed production irregularity and variability. However, the routine lacks the predictive ability to identify actual occurrence of future crops, an important issue for natural regeneration management.

DISPERSE describes the general pattern of seed dispersal for white spruce and paper birch and provides some indication of the influence winds may have upon the seed shadow. However, more information is needed to accurately model dispersal of seed upon the landscape and identify specific effects of topography and wind upon the spatial distribution of seed. For example, research regarding aspen regeneration has focused on vegetative reproduction (Peterson and Peterson 1992) and little information exists on aspen seed dispersal. Furthermore, the use of a generalized dispersal curve developed from a few stands does not necessarily reflect the dispersal trends of sites throughout interior Alaska.

The ESTABLISH routine is a very simplistic representation of the establishment process and over-generalizes the complexity of the germination, survival, growth, and establishment of seedlings. This approach was intentional, with the objective of describing seedling establishment patterns in a manner that would provide practical information to the land manager. Seed:seedling ratios provide this practicality, but the data needed to develop the proper level of detail, in terms of viable seed needed to produce an established seedling for a specific seedbed environment, is lacking. That the "best" seedbeds for germination may be different from those for survival, supports the possible need for subroutines specific to germination, first year survival, and establishment (Schupp 1995). Furthermore, representation of the spatial pattern of fire effects by DISTURB lacks empirical data. The model makes broad assumptions regarding the spatial pattern and scale of a "heterogeneous fire".

SPROUT also lacks empirical data, particularly for interior Alaska, and provides only a speculative generalized view of the vegetative reproduction process in burnt upland white spruce communities in interior Alaska.

Results

Comparison to Observations from the Rosie Creek Fire

The model was run to simulate establishment patterns of white spruce and paper birch seedlings following the Rosie Creek fire. In 1983 the Rosie Creek fire burned 3,482 ha, including one-third of the Bonanza Creek Experimental Forest (BCEF), located approximately 20 km southwest of Fairbanks (Juday and Dyrness 1985). The fire burned through both upland stands of white spruce and mixed hardwoods and poorly drained black spruce stands on the Tanana River floodplain. Fire severity was extremely variable, leaving some stands unburned and others severely burned. BCEF has been the site of extensive forest research since the late 1950's and continues currently as part of the BNZ/CPCRW Long-term Ecological Research (LTER) site. The long-term record of seed production for the area was used to simulate seed production levels (Rupp et. al. 1997), and observations of actual post-fire establishment patterns (Juday unpublished data) were used for comparison with model predictions.

The simulation involved an area of the BCEF uplands containing stands of pure white spruce and white spruce/mixed hardwoods. A 35 ha island of white

spruce/birch/aspen survived the fire and served as a major seed source (Figure 4-2). Model predictions for the period 1983 through 1987 were compared to observations of actual post-fire establishment patterns for white spruce. Two white spruce cohorts, 1983 and 1987, were identified within the disturbed area (Rupp et. al. 1997). The model predicted seedling densities for the 1983 cohort substantially higher than actually observed (Figure 4-3). The predicted densities for the 1987 cohort followed closely to those observed. The model predictions for both cohorts showed a strong correlation, 0.79 and 0.73 for the 1983 and 1987 cohorts respectively, to observed trends between seedling density and distance from the source stand.

Zasada (1985) observed first year survival of white spruce seedlings in the same general area as the 1 hectare observations. Zasada observed 1200 to 26000 first year seedlings per $100m^2$ and 200 to 1400 first year seedlings per $100m^2$ at distances of 50 and 100 m from the stand edge, respectively. Assuming 20 percent of those first year seedlings became established (Zasada et al. 1978), a range of 240 to 5200 seedlings per $100m^2$ and 40 to 280 seedlings per $100m^2$ and an average of 1520 seedlings per $100m^2$ and 160 seedlings per $100m^2$ at 50 and 100 m, respectively, would have become established. The average predicted value of established seedlings 50 m from the stand edge was 155 seedlings per $100m^2$ with a range of 0 to 1232 seedlings per $100m^2$. The average predicted value of established seedlings 100 m from the stand edge was 78 seedlings per $100m^2$ with a range of 0 to 548 seedlings per $100m^2$ (Figure 4-4).

Employing the same methods we can compare predicted and observed patterns of paper birch seedling establishment. Zasada (1985) observed paper birch first year regeneration in the same area. Using the 20 percent survival rate as in spruce (Zasada et al. 1978) an estimated average of 1120, 80, 120, and 27 seedlings per $100m^2$ at distances of 50, 100, 200, 300 m respectively, would have become established. The model predicted values of 792, 135, 19, and 2 seedlings per $100m^2$ at distances of 50, 100, 200, 300 m respectively (Figure 4-5).

Comparison to the Literature

Reports of white spruce establishment on disturbed sites in interior Alaska shows a large range in observed density levels (Zasada et al. 1978, Zasada and Grigal 1978, Zasada 1985, Wurtz and Zasada 1987, Packee 1990). Zasada (1985) working within the Rosie Creek burn observed one year old seedling densities ranging from 0 to 64800 seedlings per 100 m^2. Zasada (unpublished data) working in a clearcut with scalped and unscalped surfaces observed five year old seedling densities ranging from 0 to 11000 seedlings per 100 m^2, with significantly higher densities occurring on the scalped surfaces. Zasada et al. (1978) reported a five year old average seedling density level of 3115 seedlings per 100 m^2, on mineral soil seedbed sites within a portion of the BCEF uplands. ABFEM predicted white spruce seedling densities within the Rosie Creek burn ranging from 0 to 1232 and 0 to 239 five year old seedlings per 100 m^2, for one year and five years following the fire respectively.

Other regions of the North American boreal forest provide for only a very generalized comparison, due to significant differences in both site and environmental conditions. Studies from Canada report a range of white spruce seedling densities from 0 to over 9000 seedlings per 100 m^2 on disturbed sites (Phelps 1948, Timoney and Peterson 1996).

Sensitivity Analysis

Sensitivity analysis was conducted on individual model components. The analysis identified seed production and seedbed conditions as important controls upon seedling establishment patterns. The level of seed production directly affected subsequent seedling density and distribution across the landscape. Seed production sensitivity was explored by measuring changes in seedling establishment density under a range of production levels (Table 4-5). Establishment patterns were measured for each production level and at different occurrence times following the initial disturbance (1, 3, and 5 years following disturbance). The model predicted seedling densities at distances greater than 100 m from the seed source for both excellent and good seed years at 1, 3, and 5 years following disturbance (Figures 4-6, 4-7, and 4-8). However, relatively few of these seedlings became established, confined mainly to less than 40 m from the stand for all other production levels regardless of time since disturbance (Figures 4-6, 4-7, and 4-8).

The influence of seedbed conditions on seedling establishment success was investigated by measuring seedling density at various distances from the source under different burn severity probability scenarios (Table 4-6). There was no real difference in the overall average burn severity across the landscape, regardless of the burn scenario (Figure 4-9). Comparison of average seedling density at different distances from the seed source revealed significant differences only among the burn scenarios where the entire landscape was burned to the same severity (i.e. all cells had the same severity value). Under all three scenarios, the overall average was less than the average number of seedlings less than 50 m from the stand edge (Figure 4-10). Similarly, the average seedling density at distances greater than 80 m from the stand edge were lower than seedling densities 80 m or less from the stand edge.

The sensitivity of both seed production and seedbed receptivity highlight the importance of an accurate seed:seedling index in determining realistic establishment patterns across the landscape. The results from the Rosie Creek simulation showed a high correlation between observed and predicted values for both the 1983 and 1987 white spruce cohorts. However, actual agreement among observed and predicted seedling density, as determined by the "best guess" seed:seedling index, varied among and between cohorts. The "best guess" indexes were developed from the literature (Tables 4-3 and 4-4) and personal observations.

The white spruce seed:seedling index was systematically altered in an attempt to identify the index values that produced the best agreement between the observed and

predicted seedling densities for the Rosie Creek burn. The analysis for the Rosie Creek simulation revealed index values greater than the "best guess" index. The "best fit" index, which was 300 seeds more than the "best guess" index, produced the highest agreement between predicted and observed seedling densities (Figure 4-11).

Discussion

The successful establishment of natural regeneration is an important component of ecosystem management and sustainability. Natural regeneration is important in recolonizing naturally disturbed sites and in providing an acceptable stocking level following harvesting activities. Natural regeneration following harvesting provides genetic diversity and reduces costs associated with artificial regeneration. The natural regeneration of white spruce in interior Alaska is an important issue in current forest management. The episodic nature of white spruce seed production poses significant problems to the land manager, in terms of the ability to predict successful seedling regeneration of a site. A better understanding of interior Alaska white spruce regeneration dynamics would provide increased confidence to the land manager for implementing natural regeneration methods in white spruce management (Zasada 1995).

ABFEM provides geographically explicit information that can assist the land manager in silvicultural decisions and aid in the development of harvest layouts. The model provides output of potential use for several management issues including:

identifying areas that may not regenerate naturally, maximizing the area of potential natural regeneration success, and identifying areas needing specific site preparation and/or seedling planting.

The model realistically simulated seed dispersal and seedling establishment pattern of white spruce following the 1983 Rosie Creek fire. The overestimation of the 1983 cohort is not necessarily a failure of the model, but may be due to the relatively small sample area of the 1 hectare plot. An area of approximately 23 hectares was sampled from the model simulation versus the 1 hectare area of actual observation. The 23 hectare area most likely reflects a more representative sample of seedbed conditions, whereas the 1 hectare observation area reflects a less representative seedbed. A significant portion of the 1 hectare sample area was recolonized by *Calamogrostis canadensis* (Rupp et. al. 1997), which would tend to decrease the amount of seedlings becoming established (Youngblood 1992, Lieffers et al. 1993).

Stems of aspen and birch originating from root suckers and stump sprouts contribute to a mosaic pattern of vegetation and provide important wildlife habitat and forage. Vegetative regeneration also acts as a strong competitor, reducing the ability for white spruce seedlings to become established and/or extending the successional clock, in terms of time until a climax sere can be reached (Youngblood 1992, Coates et al. 1994). The ability to simulate more than a general view of potential site occupation patterns of vegetative regeneration is beyond the current scope of this project. However, empirical data on sprouting densities in interior Alaska could be used to

develop a more robust and predictive model, in terms of the extent and effect of vegetative reproduction on white spruce seedling establishment patterns.

Analysis of the effects of various seed production levels revealed considerable differences in establishment patterns. There were major differences in seedling establishment densities for both good and excellent production events versus moderate or poor events. Using the requirements for post harvesting stocking of 1553 seedlings/ha as a threshold determinant of natural regeneration stocking, I can compare the "effective" stocking ability of individual production events (Figure 4-12, 4-13, and 4-14). A considerable difference in establishment extent between good or excellent production events and poor or moderate events was identified. These results suggest that good or excellent production events within 5 yr of disturbance will provide adequate seedling stocking levels to a distance of 100 and 200 m from the seed source, respectively (Figure 4-15 and 4-16). Poor or moderate production events will have little impact upon the vegetation regardless of seedbed conditions.

Analysis of the sensitivity of seedbed receptivity showed a difference between establishment patterns at different distance intervals under differing seedbed conditions. Only homogeneous burn severity patterns revealed significant differences, in terms of seedling density among different distance intervals (Figure 4-10). Differences appeared between the overall seedling density average and the average density of seedlings less than 50 m from the source edge, and between seedling densities greater than 80 m from the seed source and densities 80 m or less. These results suggest that site preparation

of less than the entire area of interest or site preparation at distances of more than 80 m from the seed source will provide little benefit, in terms of natural regeneration establishment success.

The accuracy of the model predictions can be improved through the development of a more accurate seed:seedling index. Development of an index from the literature, highlighted the need for more detailed studies of seed:seedling ratios for a range of seedbed conditions. Despite these inaccuracies, the current model provides general utility in describing the patterns of seedling establishment given a particular set of circumstances. For instance, we can produce a composite map of white spruce seedling densities for a 6 yr period, upon a newly disturbed (i.e. burned) site (Figure 4-17). The potential application of the model in forest management is promising, providing the land manager with basic information important in the development of a successful silvicultural plan.

Summary

ABFEM realistically models the early establishment patterns of tree seedlings in burnt upland white spruce ecosystems in interior Alaska. The model simulates the production of seed, dispersal of seed, disturbance effects upon the seedbed, vegetative reproduction potential, and early establishment patterns of white spruce, paper birch, and aspen seedlings upon the landscape. ABFEM functioned adequately in simulating

the establishment patterns of paper birch and white spruce seedlings from seed following the 1983 Rosie Creek fire.

The modeling concept is a simplistic representation of the underlying biology of interior Alaska upland white spruce ecosystems. Lack of data for routine development and validation is a major limitation to the current model. Simulations identified information gaps and areas of needed research and empirical data. The greatest need is the development of a more detailed seed:seedling index for both white spruce and paper birch as well as additional information on seed dispersal and vegetative reproduction.

Sensitivity analysis identified seed production and seedbed receptivity as the most sensitive model components. These results identify the critical importance of the timing of seed production overlapping with a receptive seedbed. A minimum production threshold, either a good or excellent seed crop, limits seedling establishment extent and density. Seedbed receptivity is strongly tied to seed production, in terms of seedling establishment success, and only intensive forest floor disturbances provide a measurable increase in seedling spatial extent and density.

A real potential for application in forest management planning and decision making was demonstrated. The model provides the ability to simulate potential regeneration patterns upon the landscape following disturbance. Further application to forest management involves assisting in harvest layouts and maximizing the use of

regeneration capital for restocking a harvested area. Additional model development for forest management decision making seems warranted.

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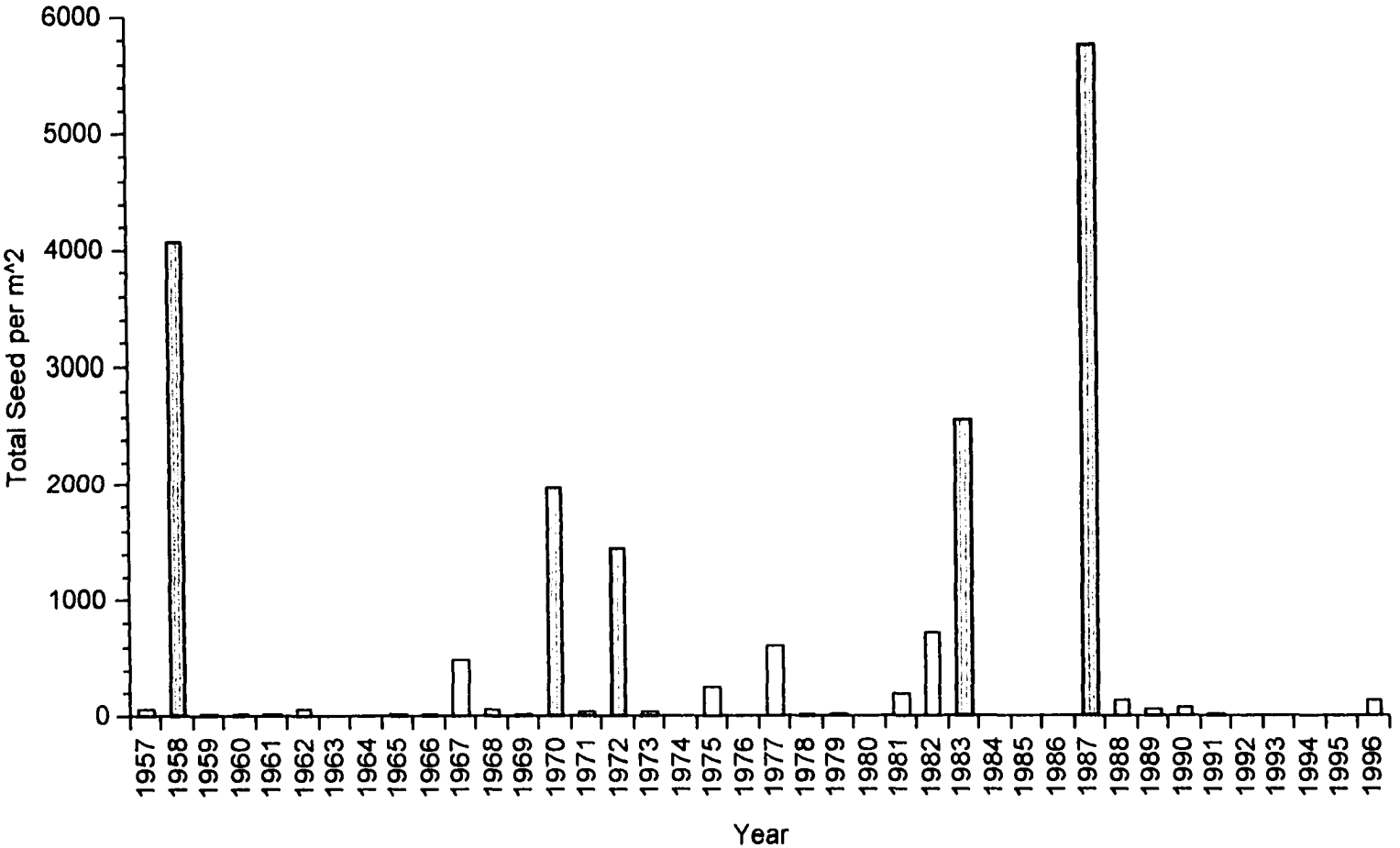

Figure 4-1. White spruce average annual within stand seed production trends from the Bonanza Creek Experimental Forest (BCEF) for the period 1957 to 1996 (Rupp et. al. 1997). Shaded bars represent exceptional production years. Average seedfall was calculated from two sites (n = 2) within BCEF.

Figure 4-2. Perspective view of the Bonanza Creek Experimental Forest (BCEF) study site and the 1983 Rosie Creek Burn.

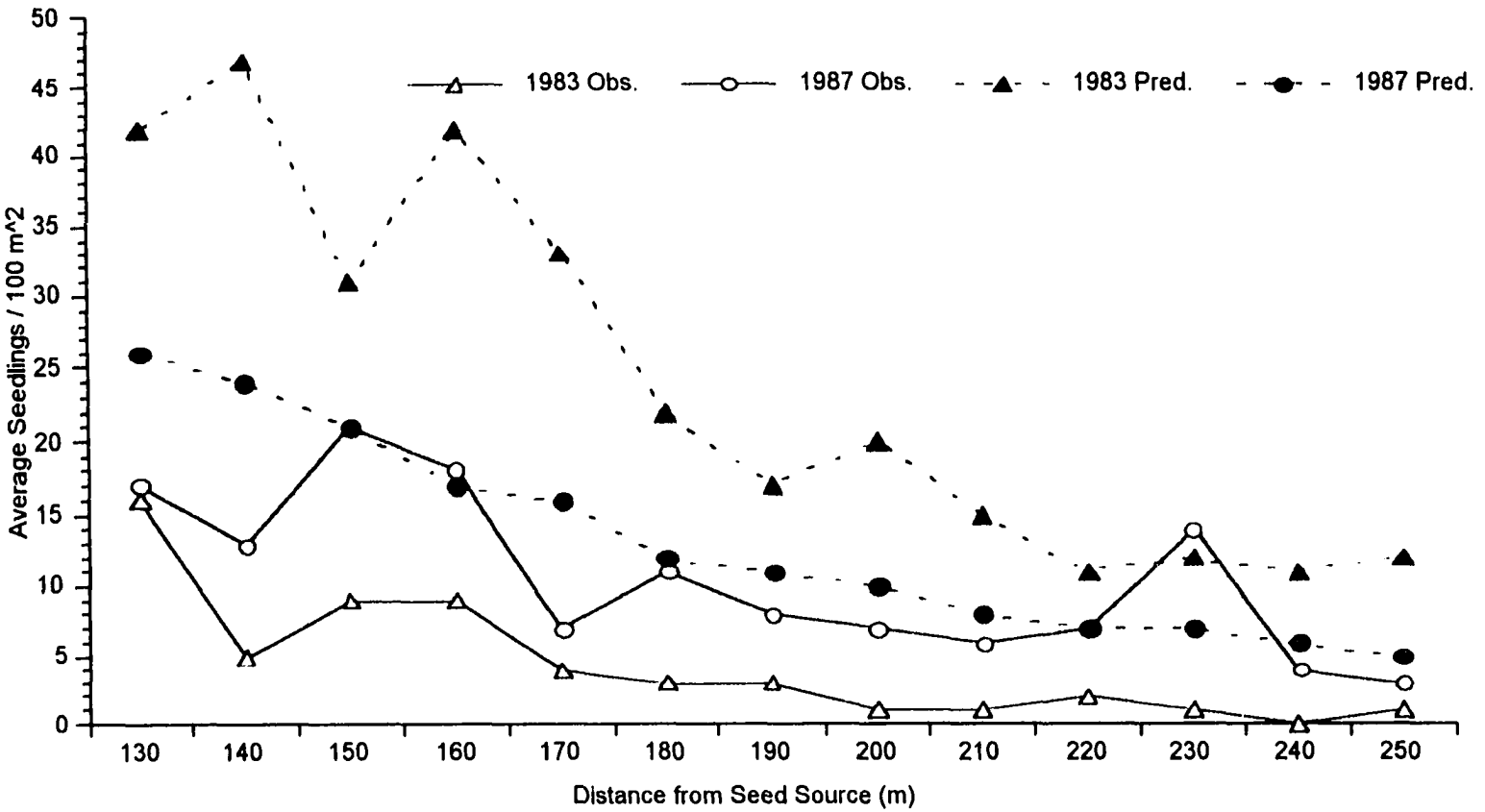

Figure 4-3. Observed (—) and predicted (----) white spruce seedling establishment patterns in the Rosie Creek burn, resulting from the 1983 (blue) and 1987 (red) seed crops. Observations were collected from a 1 ha sample plot. The model predictions were sampled from a 23 ha simulation area, using the original seed:seedling index. Seed production and dispersal data for BCEF were used as model input.

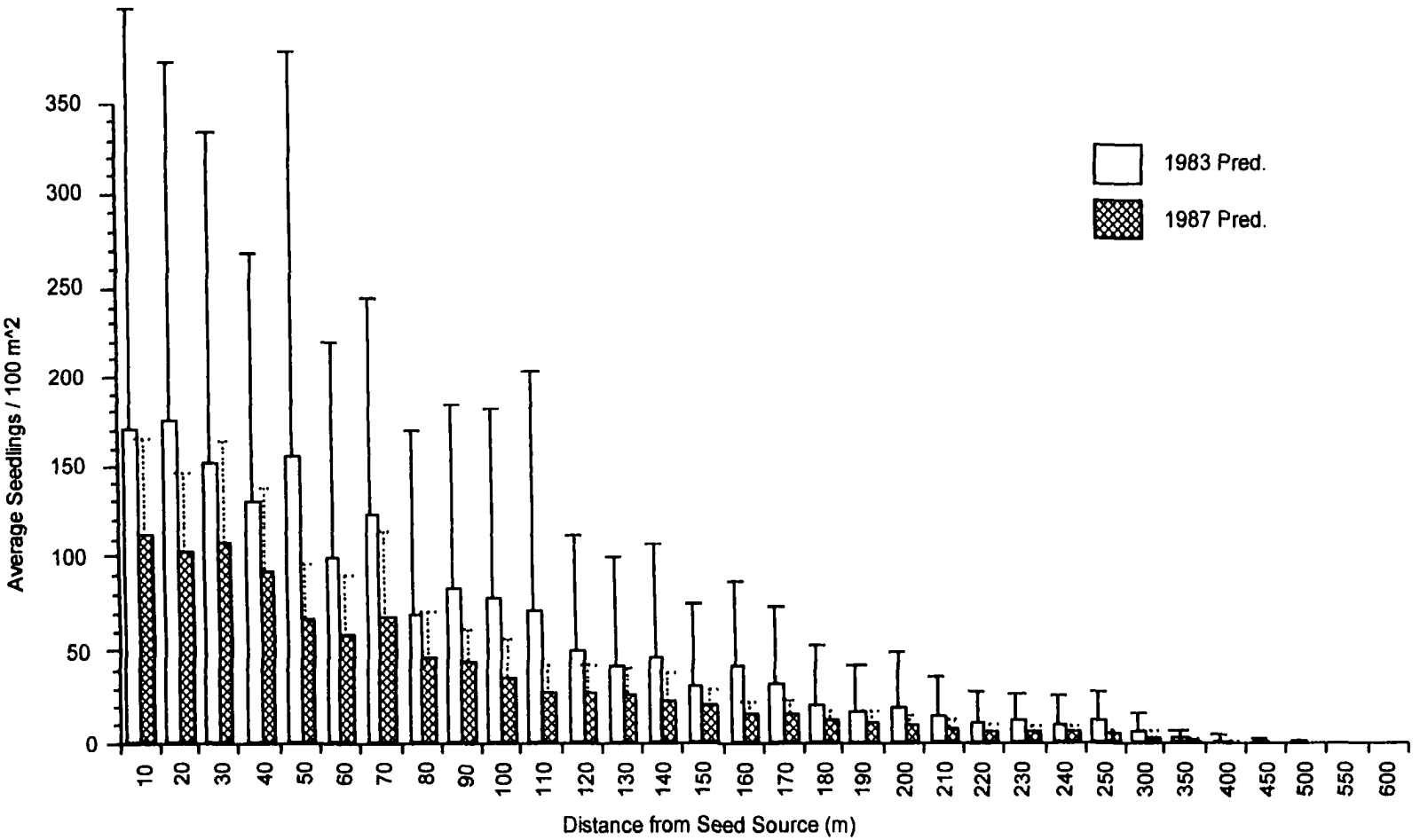

Figure 4-4. Predicted average white spruce seedling density and distance from the seed source for the 1983 (white bars) and 1987 (hatched bars) cohorts at Bonanza Creek (BCEF). Error bars represent a 95 percent confidence interval .

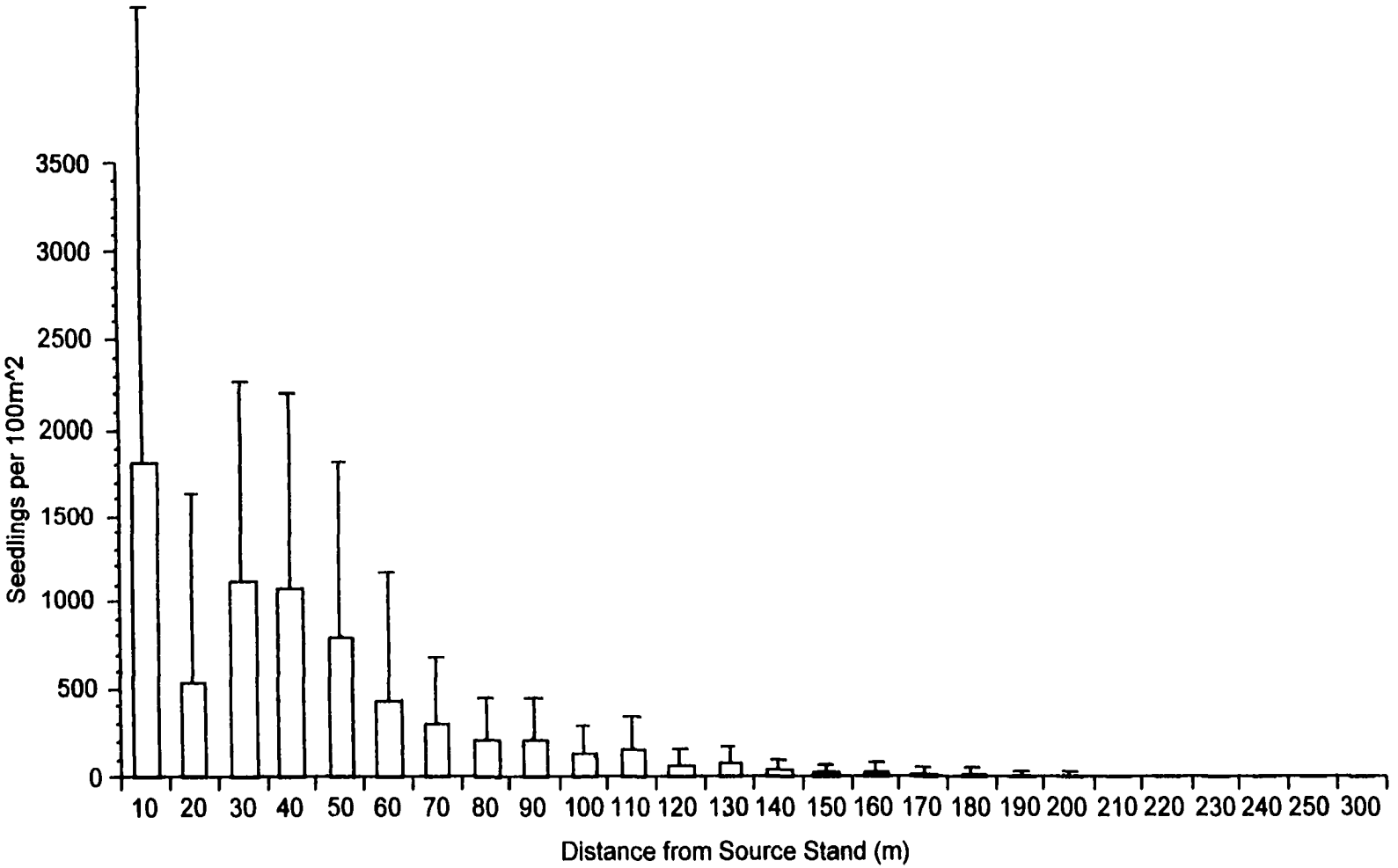

Figure 4-5. Predicted average paper birch seedling density and distance from the seed source for the 1983 cohort at Bonanza Creek (BCEF). Error bars represent a 95 percent confidence interval .

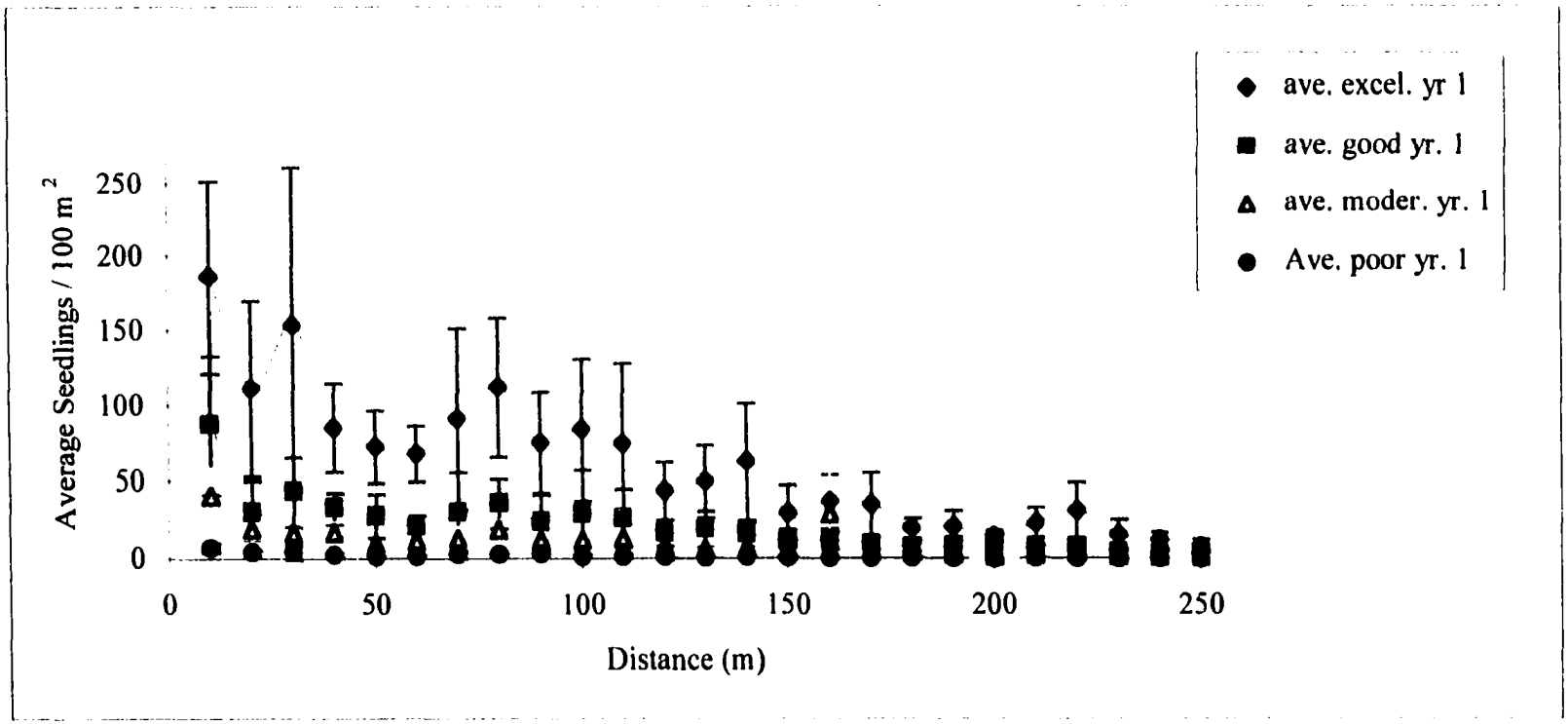

Figure 4-6. White spruce seed production sensitivity analysis showing average seedling density and distance for production events (see Table 4-5) occurring 1 yr following disturbance. Simulations were carried out for an excellent (blue), good (red), moderate (yellow), and poor (green) seed crop. Sample size was 7 cells at each distance interval (n = 7). Error bars represent a 95 percent confidence interval . Seedbed conditions were heterogeneous across the landscape (i.e. randomly distributed).

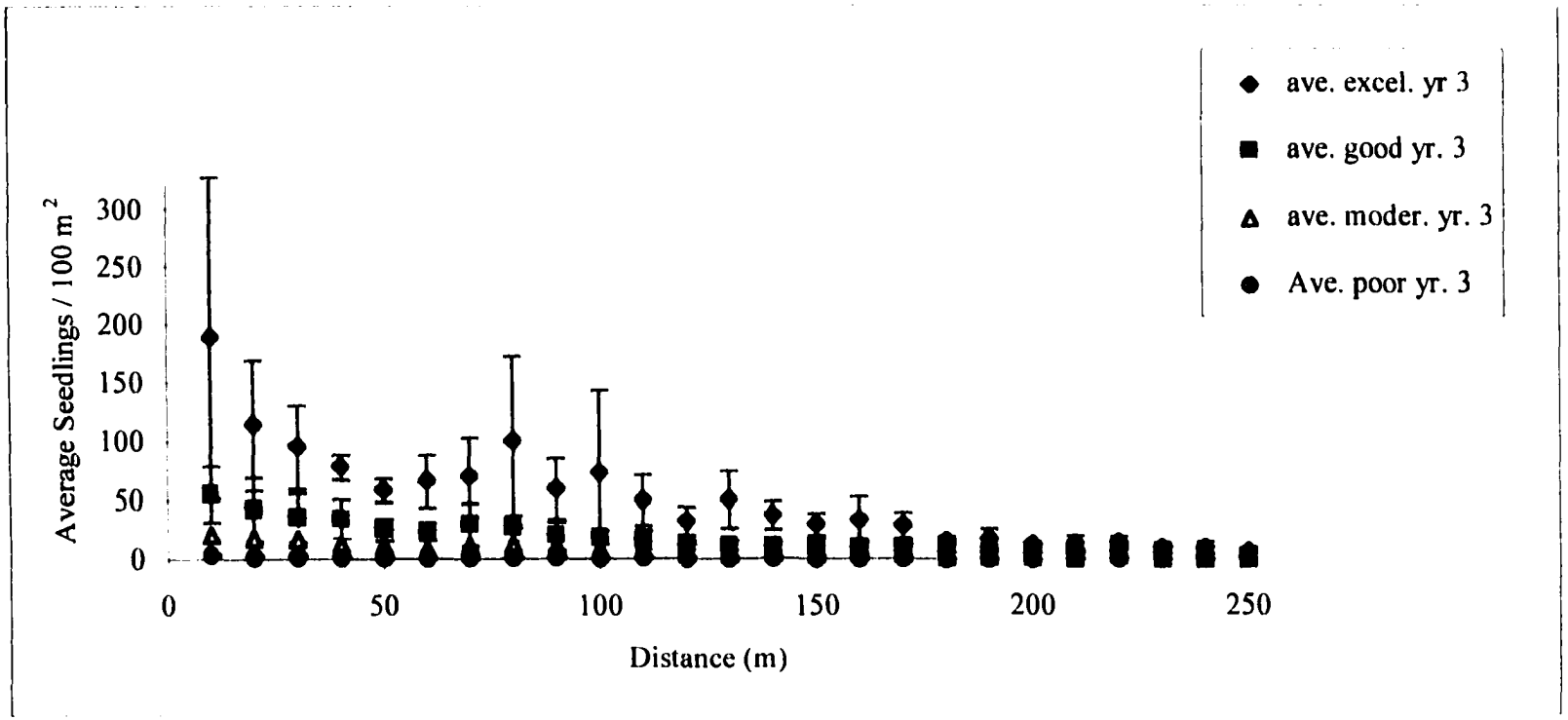

Figure 4-7. White spruce seed production sensitivity analysis showing average seedling density and distance for production events (see Table 4-5) occurring 3 yr following disturbance. Simulations were carried out for an excellent (blue), good (red), moderate (yellow), and poor (green) seed crop. Sample size was 7 cells at each distance interval (n = 7). Error bars represent a 95 percent confidence interval . Seedbed conditions were heterogeneous across the landscape (i.e. randomly distributed).

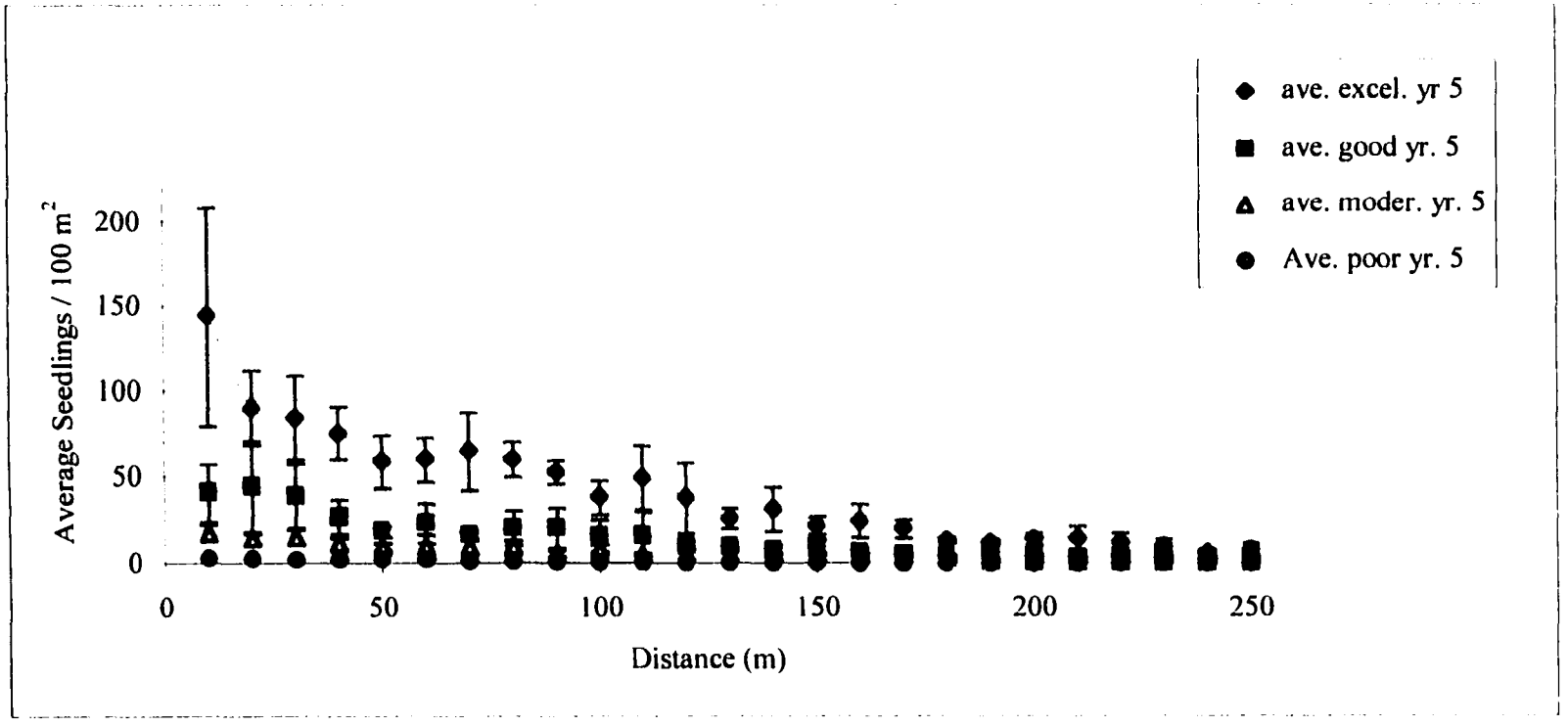

Figure 4-8. White spruce seed production sensitivity analysis showing average seedling density and distance for production events (see Table 4-5) occurring 5 yr following disturbance. Simulations were carried out for an excellent (blue), good (red), moderate (yellow), and poor (green) seed crop. Sample size was 7 cells at each distance interval (n = 7). Error bars represent a 95 percent confidence interval . Seedbed conditions were heterogeneous across the landscape (i.e. randomly distributed).

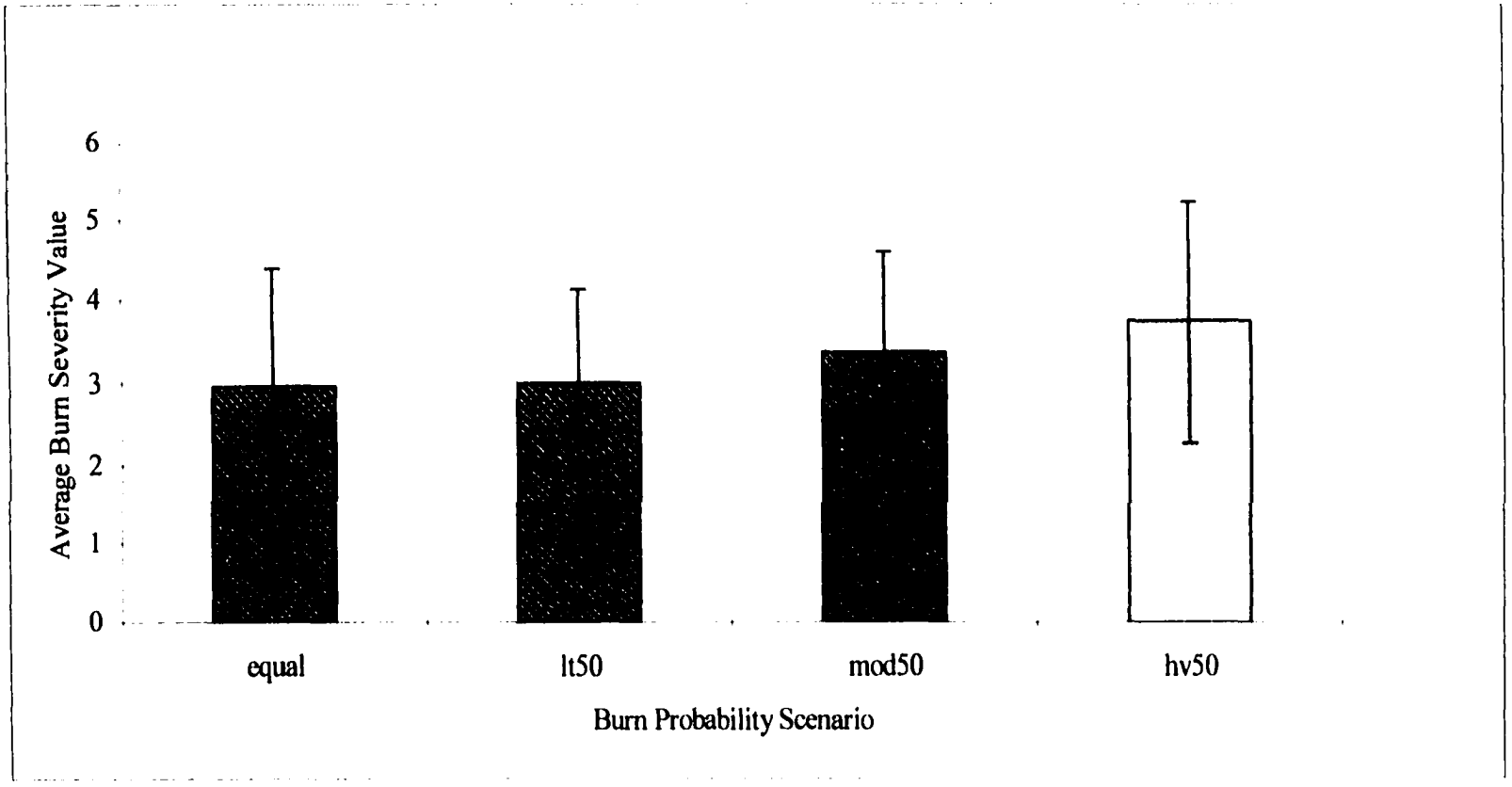

Figure 4-9. Average simulated burn severity class across the landscape for scenarios of equal burn severity probabilities and 50 percent probability of a light, moderate, or heavy burn severity. Sample size was 8 ha and error bars represent a 95 percent confidence interval ..

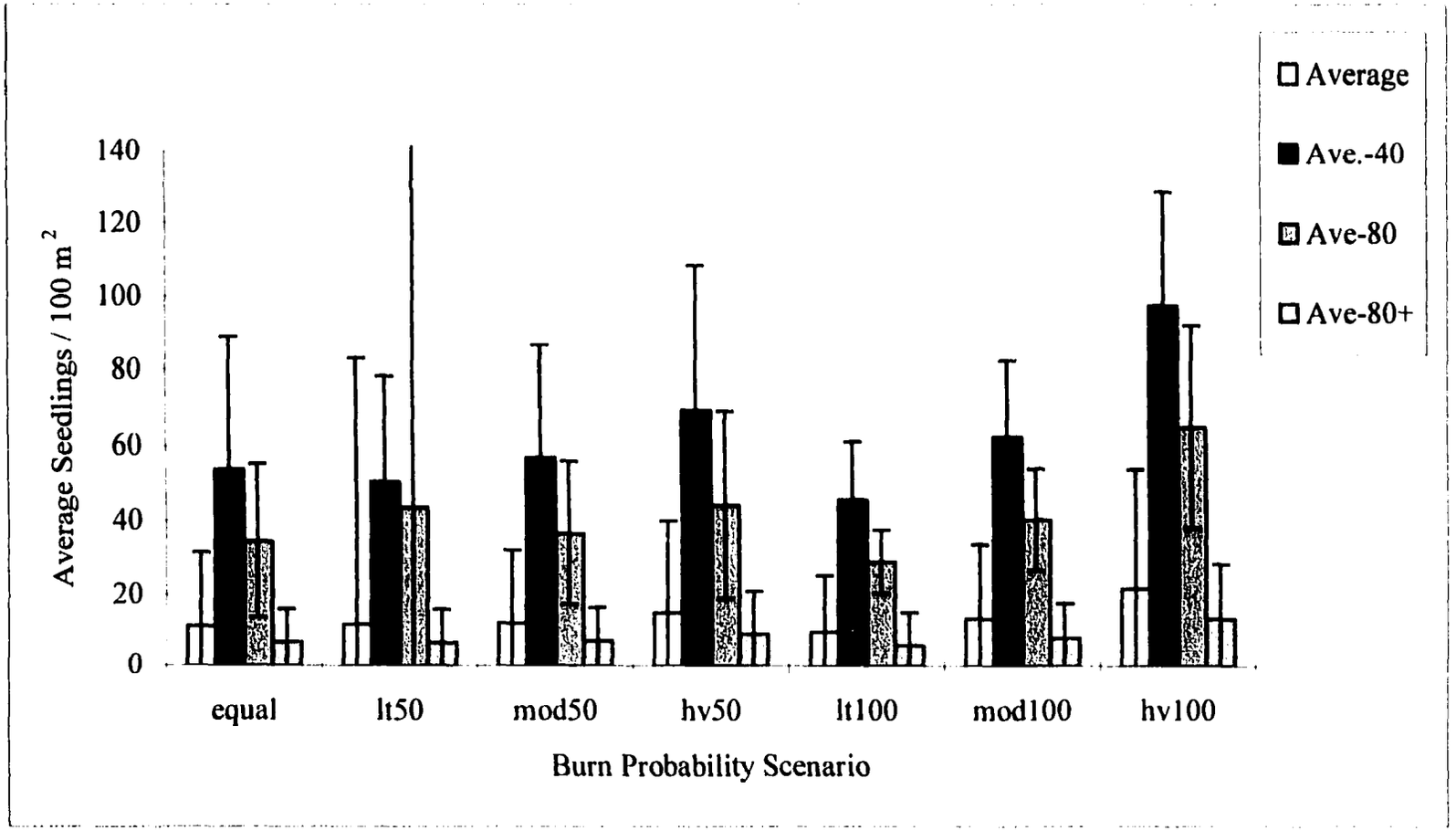

Figure 4-10. Average simulated seedling densities across the landscape under different burn severity probability scenarios (see Table 4-6). Sample size was 8 ha and error bars represent a 95 percent confidence interval. Overall average (white), less than 40 m (dark), less than 80 m (gray), and greater than 80 m (lt. gray) from the stand edge. Simulation represents seedlings establishing from a good production event (1200 seeds/m^2) occurring 1 yr following disturbance.

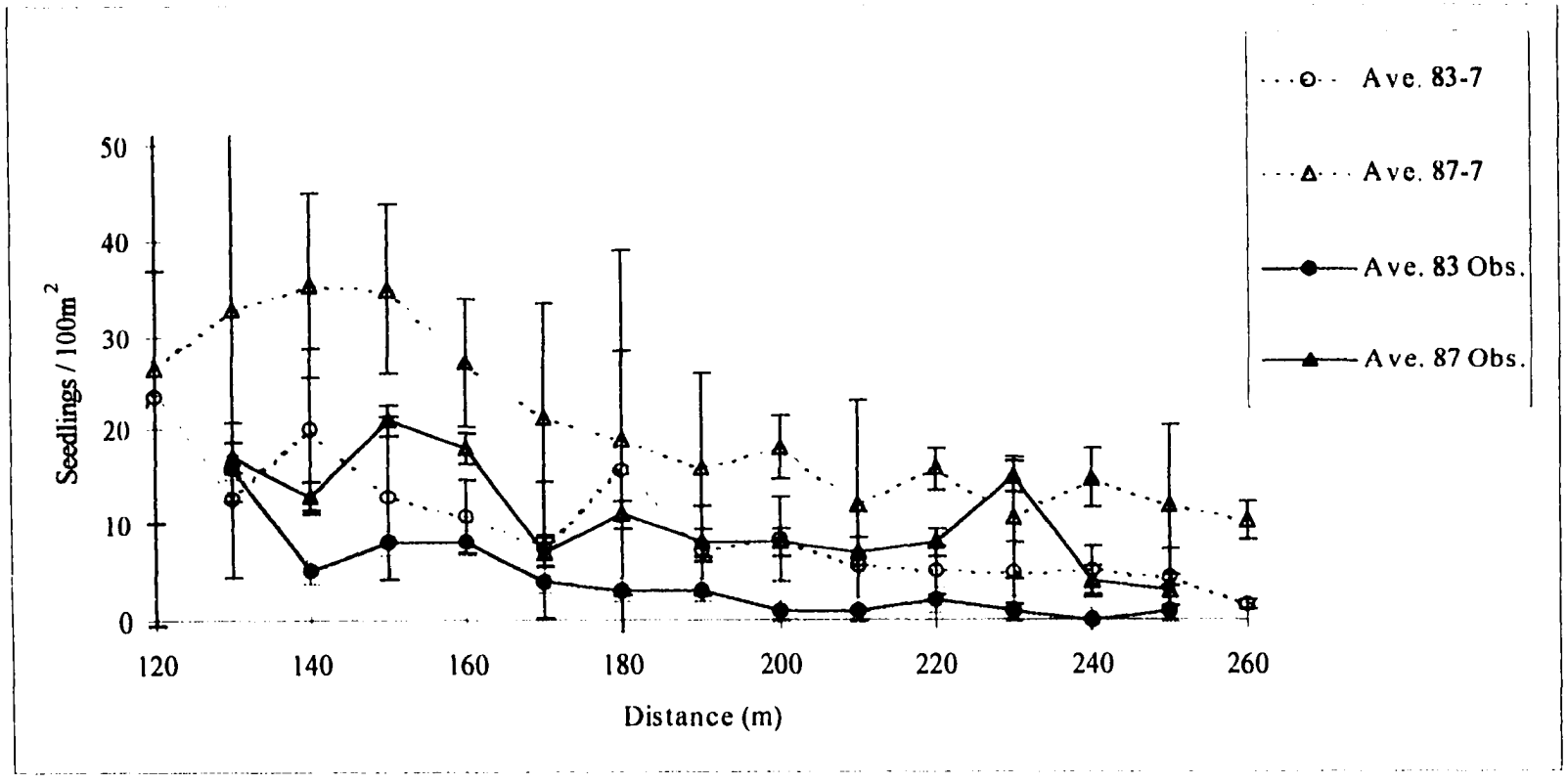

Figure 4-11. Observed (——) and predicted (-----) white spruce seedling establishment patterns in the Rosie Creek burn, resulting from the 1983 (blue) and 1987 (red) seed crops. Observations were collected from a 1 ha sample plot. The model predictions were sampled from a 23 ha simulation area, using the calibrated "best fit" seed:seedling index (see Table 4-7). Seed production and dispersal data for BCEF were used as model input.

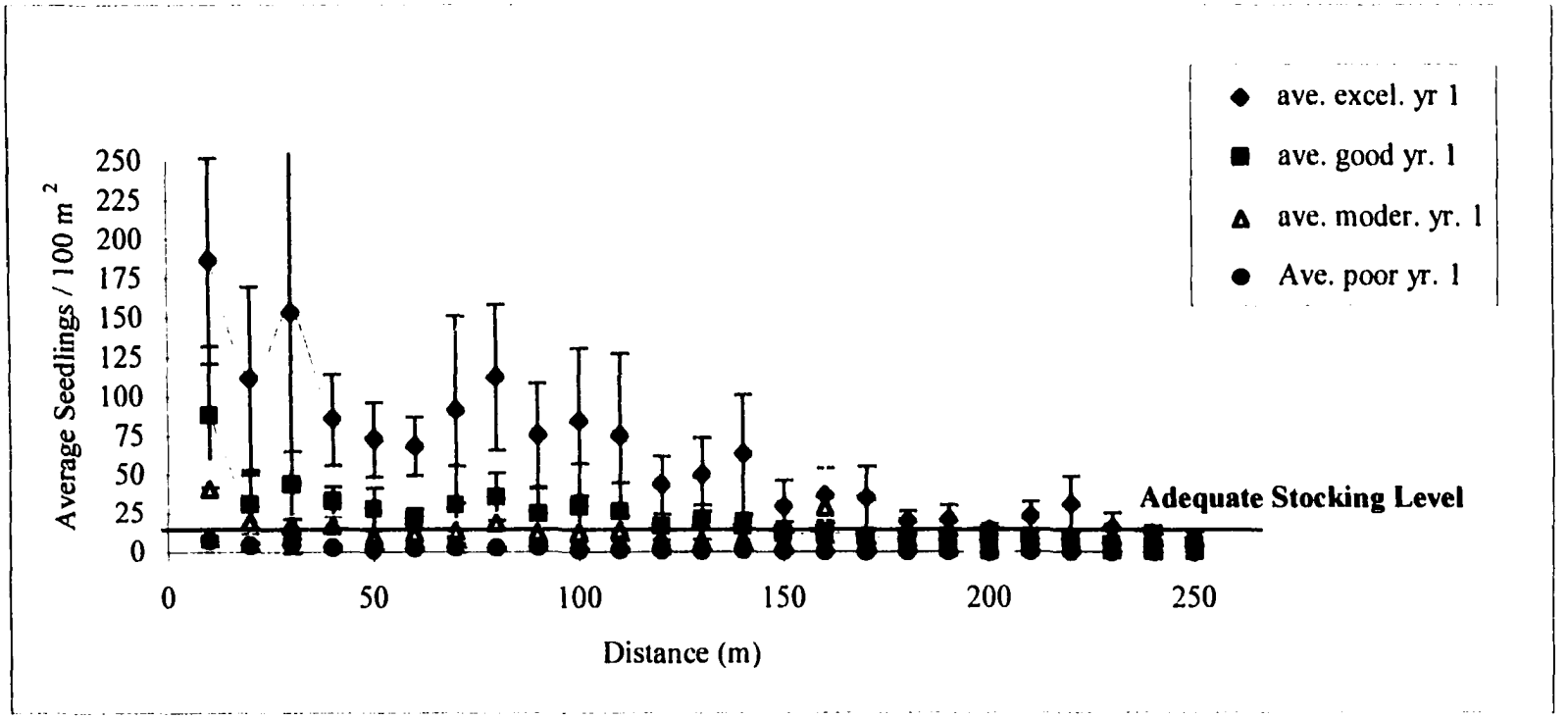

Figure 4-12. White spruce average seedling density and distance for production events (see Table 4-5) occurring 1 yr following disturbance. Simulations were carried out for an excellent (blue), good (red), moderate (yellow), and poor (green) seed crop. The adequate stocking level represents the threshold distance at which 1553 seedlings/ha become established. Sample size was 8 ha. Error bars represent a 95 percent confidence interval . Seedbed conditions were heterogeneous across the landscape (i.e. randomly distributed).

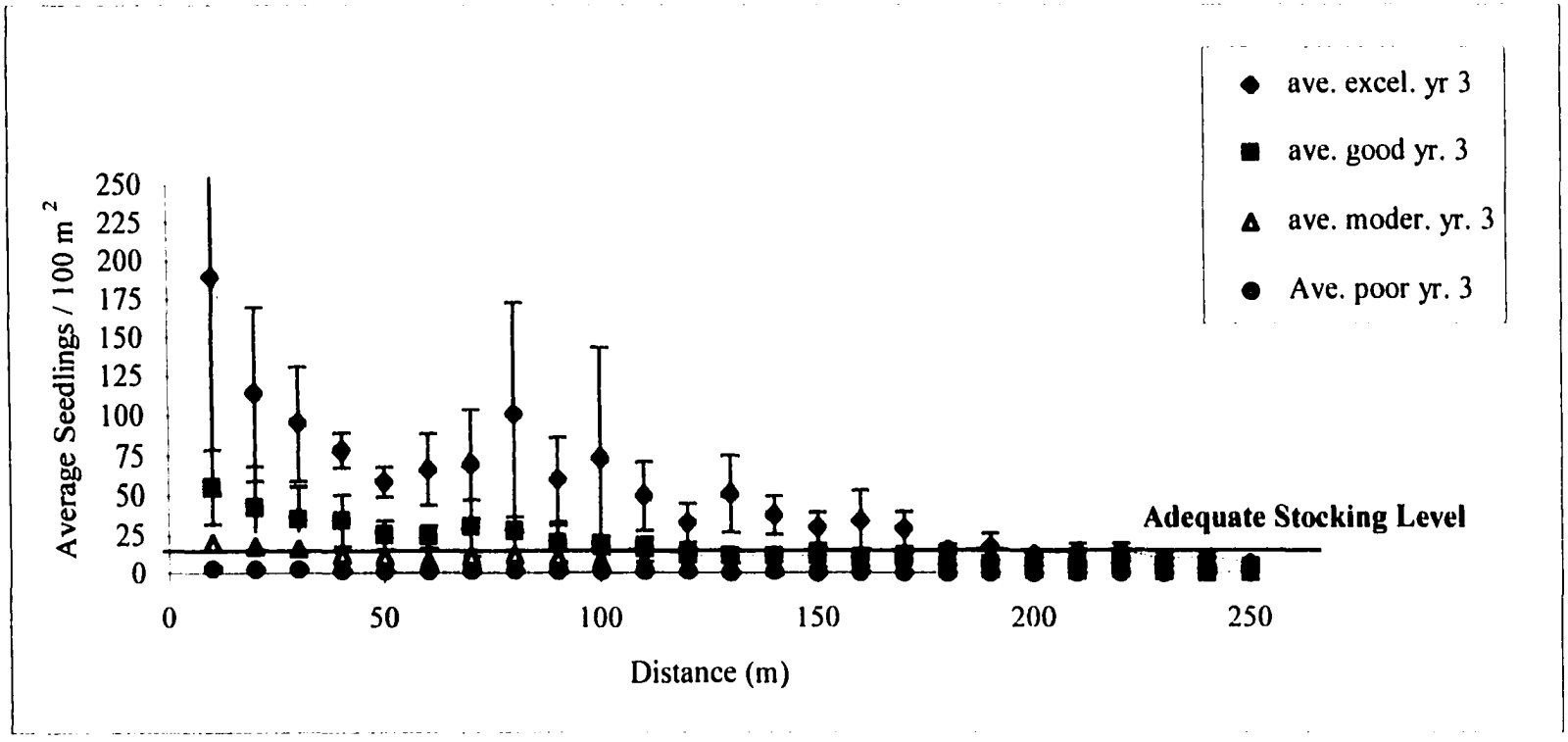

Figure 4-13. White spruce average seedling density and distance for production events (see Table 4-5) occurring 3 yr following disturbance. Simulations were carried out for an excellent (blue), good (red), moderate (yellow), and poor (green) seed crop. The adequate stocking level represents the threshold distance at which 1553 seedlings/ha become established. Sample size was 8 ha. Error bars represent a 95 percent confidence interval . Seedbed conditions were heterogeneous across the landscape (i.e. randomly distributed).

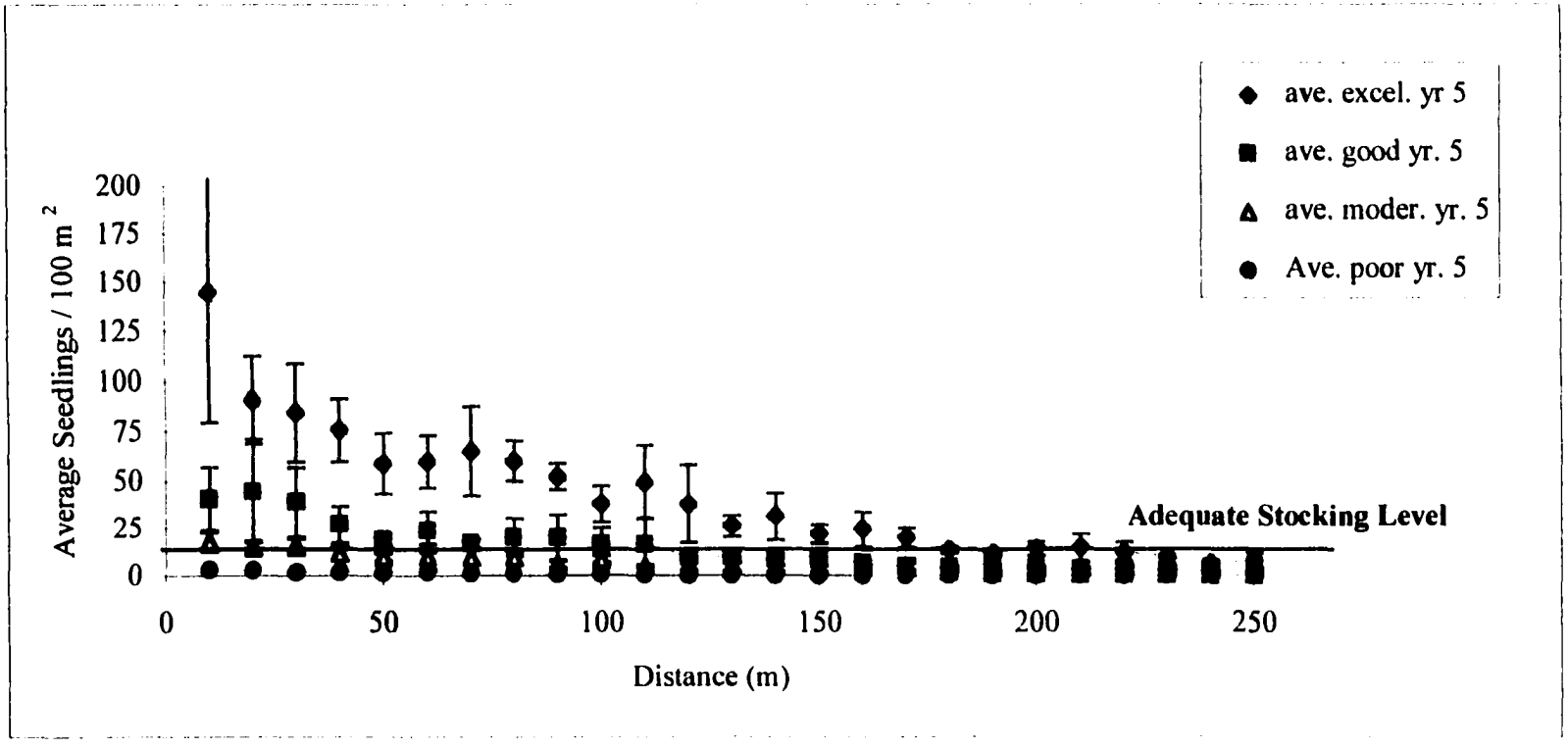

Figure 4-14. White spruce average seedling density and distance for production events (see Table 4-5) occurring 5 yr following disturbance. Simulations were carried out for an excellent (blue), good (red), moderate (yellow), and poor (green) seed crop. The adequate stocking level represents the threshold distance at which 1553 seedlings/ha become established. Sample size was 8 ha. Error bars represent a 95 percent confidence interval . Seedbed conditions were heterogeneous across the landscape (i.e. randomly distributed).

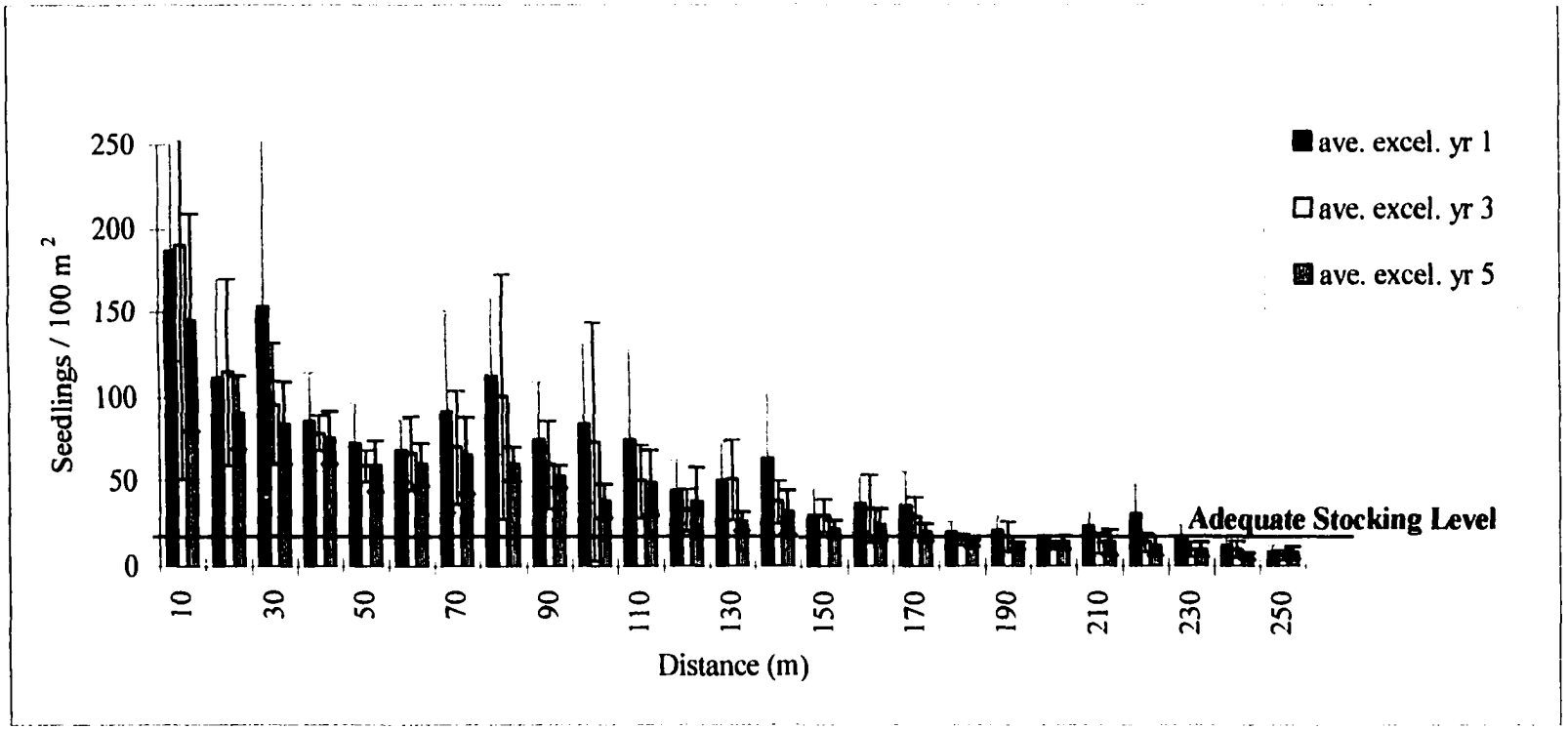

Figure 4-15. White spruce seedling establishment pattern resulting from an excellent production (3000 seeds/m^2) event 1 (dark bars), 3 (white bars), and 5 (hatched bars) yr following fire. The adequate stocking level represents the threshold distance at which 1553 seedlings/ha become established. Sample size was 8 ha. Error bars represent a 95 percent confidence interval . Seedbed conditions were heterogeneous across the landscape (i.e. randomly distributed).

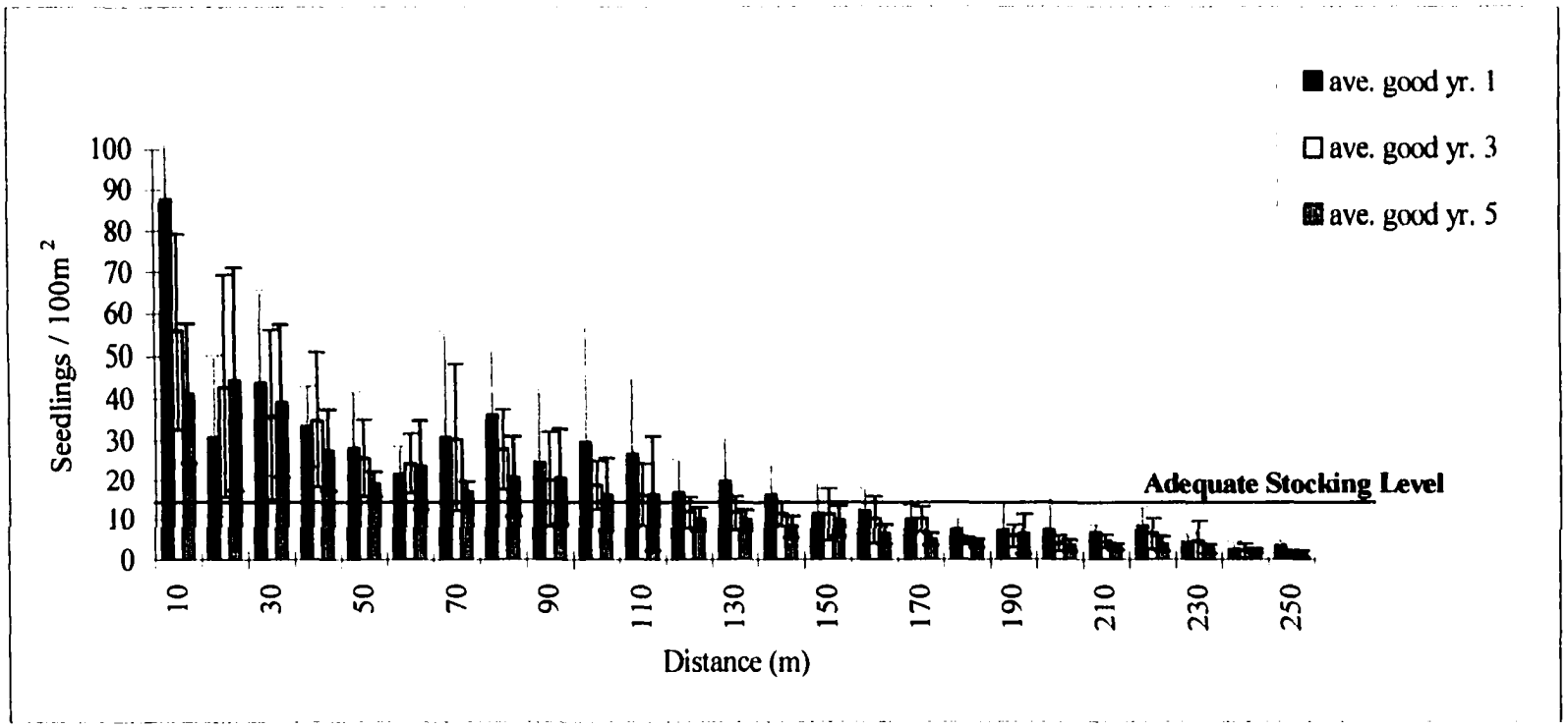

Figure 4-16. White spruce seedling establishment pattern resulting from a good production (1000 seeds/m^2) event 1 (dark bars), 3 (white bars), and 5 (hatched bars) yr following fire. The adequate stocking level represents the threshold distance at which 1553 seedlings/ha become established. Sample size was 8 ha. Error bars represent a 95 percent confidence interval . Seedbed conditions were heterogeneous across the landscape (i.e. randomly distributed).

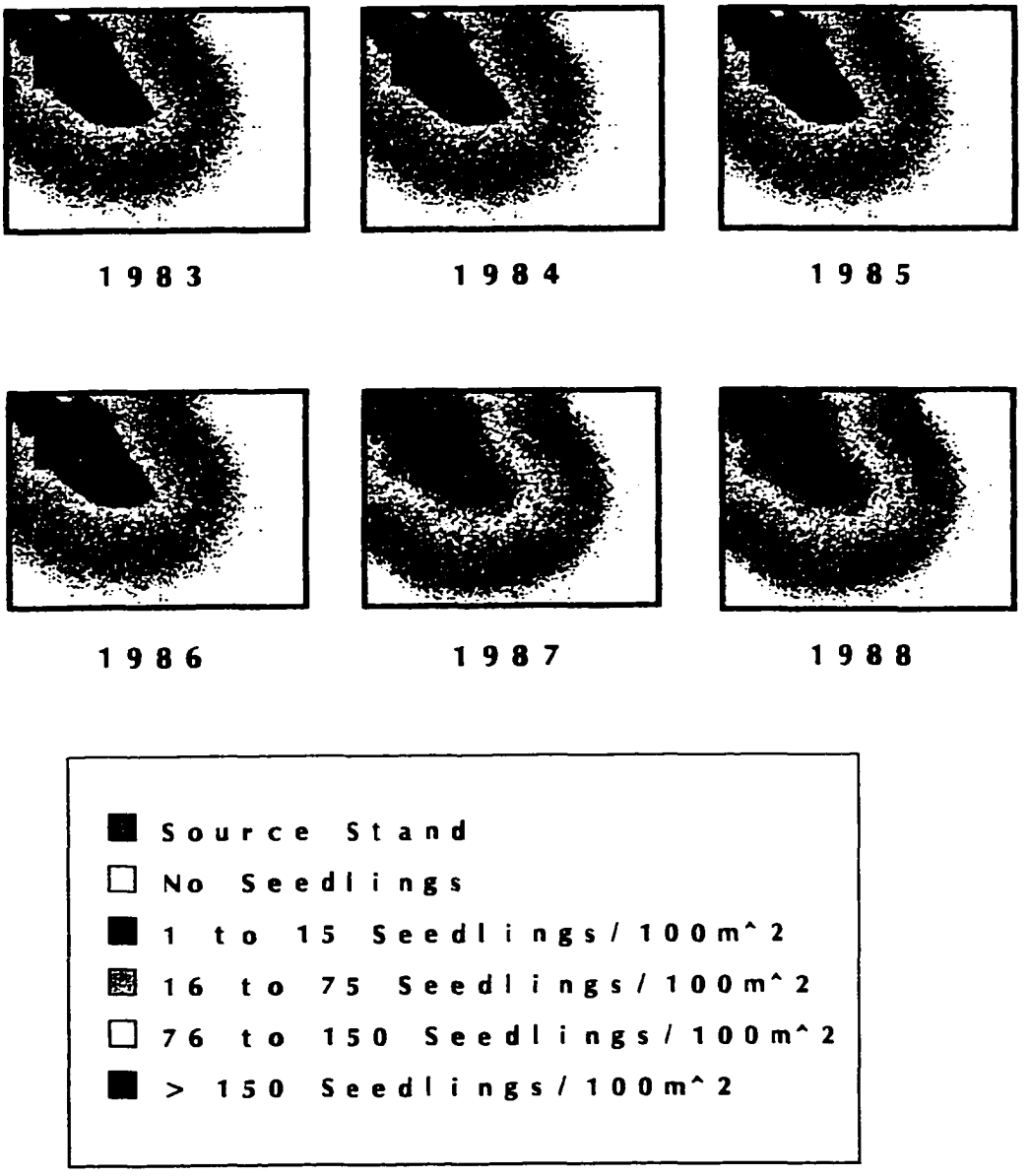

Figure 4-17. Composite map of predicted natural seedling regeneration pattern for a 6 yr simulated period (1983-1988) at Bonanza Creek (BCEF).

Table 4-1. Observed (Rupp et al. 1997) and predicted white spruce seed production trends for Bonanza Creek Experimental Forest. Period of observation was 1957-1995. Model predictions represent the average of 100 replicate 40 yr runs. Increased and decreased probability predictions represent a 10 percent increase and decrease in seed production success, respectively.

	Observed[1]	Predicted	Predicted[2] (Increased)	Predicted[3] (Decreased)
Poor Rating				
ave. seed/m^2	27.80	30.96	30.36	30.42
std. deviation	24.00	20.23	20.58	19.73
Mod. - Good Rating				
ave. seed/m^2	433.90	427.58	436.78	442.98
std. deviation	233.40	226.40	219.12	219.96
Excellent Rating				
ave. seed/m^2	3001.80	3167.46	3185.95	3159.65
std. deviation	1860.80	1754.45	1722.45	1754.89
# of Excellent Yrs.				
mean	5	4.26	7.79	1.03
std. deviation	—	1.86	1.98	0.99
Interval Between Excellent Yrs.				
mean	7	7.02	3.96	12.28
std. deviation	—	5.05	1.56	8.50
# of Successful Yrs.				
mean	11	10.74	15.06	3.60
std. deviation	—	2.68	2.66	1.69

[1] Statistics for observed production trends from Rupp et. al. (1997).
[2] Model predictions under 10 % increased probability of successful seed production events.
[3] Model predictions under 10 % decreased probability of successful seed production events.

Table 4-2. Dynamic seed:seedling index for white spruce on (a) northerly aspects and (b) southerly aspects. Represent the average number of viable white spruce seed needed to produce one 5 yr old free to grow seedling on a given seedbed substrate and at a given time since initial disturbance.

(a)

	Initial Burn Severity				
Time[1]	Unburned	Scorched	Light	Medium	Heavy
1 Yr	2200	2000	1400	500	100
2 Yr	2200	2200	1600	1000	250
3 Yr	2200	2200	1800	1600	500
4 Yr	2200	2200	2000	1800	1000
5+ Yr	2200	2200	2200	2000	1600

(b)

	Initial Burn Severity				
Time[1]	Unburned	Scorched	Light	Medium	Heavy
1 Yr	2500	2300	1500	750	500
2 Yr	2500	2500	1900	1500	1000
3 Yr	2500	2500	2100	1900	1300
4 Yr	2500	2500	2300	2100	1700
5+ Yr	2500	2500	2500	2300	1900

[1] indicates time since disturbance

Table 4-3a. Seed:seedling ratios for white spruce as reported in the literature. Seed:seedling ratio represents the number of viable seed needed to produce a seedling of a given age on a given seedbed substrate.

Species	Study Location	Vegetation Type	Seedbed Substrate	Seedling Age	Seed:Seedling Ratio	Reference
P. glauca	Alberta	Subalpine Forest	Mineral Soil	3 yr	11-42	Ackerman (1957)
			Mineral Soil	5 yr	13-67	
			Organic	-----	228	
	Central BC	*P. glauca*	Mineral Soil	4 yr	6-9	Eis (1967)
		A. lasiocarpa	Organic		800-1000	
	Alaska	-----	Mineral Soil	-----	24-48	Zasada (1971)
	Alaska	*P. glauca*	Mineral Soil	3 yr	18	Zasada et al. (1978)
			Mineral Soil	5 yr	21	
			Organic	3 yr	31	
	Alaska	Vegetated Silt	Mineral Soil	3 yr	24	Walker (1985),
			Organic		21	Walker
		Salix	Mineral Soil	3 yr	43	et al. (1986),
			Organic		32	Zasada et al. (1992)
		Alnus incana	Mineral Soil	3 yr	151	
			Organic		600+	
		P. balsamifera	Mineral Soil	3 yr	151	
			Organic		600+	
		P. glauca	Mineral Soil	3 yr	121	
			Organic		600	

Table 4-3b. Seed:seedling ratios for white spruce as reported in the literature. Seed:seedling ratio represents the number of viable seed needed to produce a seedling of a given age on a given seedbed substrate.

Species	Study Location	Vegetation Type	Seedbed Substrate	Seedling Age	Seed:Seedling Ratio	Reference
P. glauca	Alaska	*P. glauca*	Mineral Soil	5 yr	8-16	Zasada (Unpublished
			Mineral Soil	13 yr	9-18	Manuscript)
			Organic		68-176	
	Alaska	*P. mariana* (burned)	Mineral Soil (burned)	1 yr	476-625	Clautice (1974)
						Ganns (1977)
	Alaska	*P. glauca* (clearcut)	Mineral Soil	1 yr	15	
			Organic		31	
			Mineral Soil	2 yr	16	
			Organic		33	

Table 4-4. Seed:seedling ratios for paper birch as reported in the literature (continued). Seed:seedling ratio represents the number of viable seed needed to produce a seedling of a given age on a given seedbed substrate.

Species	Study Location	Vegetation Type	Seedbed Substrate	Seedling Age	Seed:Seedling Ratio	Reference
B. papyrifera	New Hampshire	N. Hardwood Forest	Leaf Litter	1 yr	67	Marquis et al. (1964)
			Humus		17	
			Mineral Soil		7	
	New York	N. Hardwood Forest	Mineral Soil	1 yr	5-67	Horsley and Abbott (1970)
			Mineral Soil	2 yr	11-100	
	-----	-----	Mineral Soil	1 yr	20-400	Zasada (1971)
	Alaska	*P. mariana* (burned)	Mineral Soil (burned)	1 yr	39-250	Clautice (1974
	Alaska	*P. glauca*	Organic	1 yr	13	Zasada et al (1978)
			Organic	3 yr	283	
	Alaska	*P. mariana* (burned)	Mineral Soil (burned)	3 yr	22	Zasada et al (1983)
	Alaska	*P. glauca*	Mineral Soil (burned)	1 yr	45	Zasada (1985), Perala and Ahn (1992)
	-----	-----	-----	5 yr	810	Perala (1987)

Table 4-5. Within stand white spruce seed density used for the production sensitivity experiments.

Production Level	Seeds / 100 m^2
Excellent	300,000
Good	100,000
Moderate	50,000
Poor	1,000

Table 4-6. Burn severity probability scenarios used for the seedbed sensitivity experiments.

Burn Scenario	No burn	Scorched	Light burn	Moderate burn	Heavy burn
Equal	20 percent	20 percent	20 percent	20 percent	20 percent
Light 50%	12.5 percent	12.5 percent	50 percent	12.5 percent	12.5 percent
Moderate 50%	12.5 percent	12.5 percent	12.5 percent	50 percent	12.5 percent
Heavy 50%	12.5 percent	12.5 percent	12.5 percent	12.5 percent	50 percent
Light 100%	--	--	100 percent	--	--
Moderate 100%	--	--	--	100 percent	--
Heavy 100%	--	--	--	--	100 percent

CHAPTER 5 - CONTROLS UPON NATURAL REGENERATION IN INTERIOR ALASKA: MODELING UPLAND WHITE SPRUCE ECOSYSTEMS

Introduction

The boreal forest of interior Alaska is a mosaic of vegetation representing different stages of primary and secondary succession (Van Cleve and Viereck 1981). Terrestrial landscapes are composed of a mosaic of heterogeneous land forms, vegetation types, and land uses (Urban et al. 1987). The driving variables of landscape pattern formation include disturbance, biotic processes, and environmental constraints (Levin 1978). The heterogeneous nature, both spatially and temporally, of ecosystem controls is apparent in the vegetation mosaic characteristic of the interior Alaska boreal forest. This mosaic pattern is the result of the interactions between the frequency and type of disturbance and state factor controls. State factors are variables independent of the ecosystem that determine ecosystem development (Jenny 1980). The state factors of time, parent material, topography, biota, and climate, condition ecosystem controls (Figure 5-1) that influence system structure and function (Van Cleve et al. 1991,1996). Ecosystem controls change through time (Van Cleve et al. 1991) and are spatially variable, reflecting the inherent heterogeneity of the landscape.

Natural disturbance plays a central role in determining the course of ecosystem development in interior Alaska (Van Cleve et al. 1996). A disturbance is a discrete,

punctuated killing, displacement, or damaging of one or more individuals that directly creates an opportunity for new individuals to become established (Sousa 1984). Fluvial processes of erosion, inundation, and sedimentation act upon the floodplain systems creating both primary and secondary successional trajectories. Fire may also play a role within the backswamp and meander belt areas of river floodplains (Van Cleve and Viereck 1981, Mann et al. 1995). Fire is the primary disturbance that resets the successional clock in the uplands (Van Cleve et al. 1991). The frequency and severity of fire are major influences on vegetation structure, composition, and productivity (Yarie 1981).

Fire holds a hierarchical role within the disturbance regime of interior Alaska. Yarie (1981) calculated fire cycles on the order of 50-100 years for interior Alaska forests. Other disturbances occur within these fire cycles, acting at scales from the individual tree to the landscape-level. Disturbance events such as snow breakage (Van Cleve and Zasada 1970, Sampson and Wurtz 1994) and insect attack (Holsten et al. 1985, Holsten 1990) may occur several times between fires. The timing of these events is influenced by fire, and fire is subsequently affected by the timing and severity of these other disturbance events. Herbivore browsing by both small (Bryant 1987) and large (Molvar et al. 1993) mammals can have significant impact on the vegetation and influence successional pathways, shifting community composition towards unbrowsed species (Pastor and Naiman 1992, Kielland et al. 1997).

Plants utilize various strategies or modes of reproduction to become established, increase post-establishment abundance, and survive disturbance and environmental change (Wagner and Zasada 1991). The general reproductive strategies exhibited by species take advantage of specific effects of the disturbance regime characteristic of the ecosystem. Species have evolved particular strategies that best exploit their regeneration niche, as defined by Grubb (1977). This exploitation is evident with regards to the tree species of interior Alaska. For example, the semiserotinous cones of black spruce allow for immediate stand replacement following fire.

Natural regeneration of interior Alaska forests is both spatially and temporally variable. Temporal variation results from processes and factors that control episodic seed production and changing seedbed conditions, while spatial variation includes factors of seed dispersal distance and pattern of forest floor conditions upon the landscape (Zasada et al. 1992). Reproductive strategies can be categorized into either sexual or vegetative reproduction. Sexual reproduction (Figure 5-2) involves the availability of reproductive buds and the subsequent production and dispersal of seeds. Vegetative reproduction (Figure 5-3) involves both clone expansion and regrowth from basal buds, roots, or stem segments (Zasada et al. 1992).

All interior Alaska tree species produce seed, with frequency and quantity being highly variable both within and among particular species. Aspen and birch exhibit typical characteristics of pioneering species producing large quantities of seed,

frequently, at a relatively young age that disperse long distances (Zasada 1986). This strategy allows for rapid occupation of newly disturbed sites. White spruce produce episodic bumper seed crops, up to 12 years apart, with limited dispersal (Zasada and Gregory 1969, Zasada 1971, Coates et al. 1994, Zasada 1995). White spruce bumper crops may be initiated by warm, dry climatic conditions during bud formation, which are the same conditions associated with large fire years, allowing exploitation of newly disturbed sites (Lutz 1956, Zasada 1971, Viereck 1973). Black spruce cones are semiserotinous, allowing for both yearly production and long-term retention of seed. Each of these strategies allows particular species to exploit post-disturbance conditions and maximize their regenerative potential. Important factors related to success of the sexual reproduction strategies, with regards to successful establishment, involve issues related to the seed rain and environmental factors influencing the seedbed. The timing, quantity and quality, and effective dispersal distances of the seed crop are important seed rain issues that directly affect subsequent seedling establishment.

Vegetative reproduction is important during both primary and secondary succession (Zasada et al. 1992). This strategy allows an individual plant to take advantage of an established root system, enabling the individual to immediately exploit post-disturbance conditions and gain a competitive advantage. Paper birch employs basal buds as its chief vegetative source for regeneration, whereas aspen utilize adventitious root buds to vigorously resprout following disturbance. The relative success of both these strategies is directly influenced by the type and severity of

disturbance. For example, severe fires may damage or kill the bud bank reducing the probability of vegetative regeneration.

Paper birch and aspen employ both sexual and vegetative strategies, whereas white spruce principally reproduces sexually. These strategies may occur simultaneously within a site and the relative importance of each in recolonizing the site will depend upon species composition, site conditions, and severity of disturbance (Zasada et al. 1992). Detailed descriptions of these strategies for boreal forest species can be found in Zasada (1971, 1986) and Zasada et al. (1992). The interaction between the disturbance regime and reproductive strategy is complex. This interaction is particularly important with regards to seedling establishment patterns in the Alaskan boreal forest. For example, the episodic production of white spruce seed and seedbed receptivity must coincide in a 5 year window of opportunity for the successful establishment of a new white spruce cohort. The coupling of disturbance regime and reproductive strategy provides information important in determining successional pathways.

The purpose of this chapter is to describe controls over early seedling establishment patterns in upland white spruce ecosystems of interior Alaska and identify how this information can be utilized in forest management. Synthesizing information on regeneration dynamics of interior Alaska tree species through simulation modeling can provide the land manager with information on natural regeneration of white spruce that can reduce dependence upon planting to regenerate disturbed sites.

Controls Upon Early Seedling Establishment Patterns

Regeneration via seed allows for both the continuation and establishment of communities, is responsible for change in floristic composition of communities, and provides genetic variability for species adaptation (Farmer 1997). Understanding controls upon natural regeneration of white spruce from seed is an important forest management issue for interior Alaska. The persistence and management of white spruce is both a commercially and socially important component of the boreal forest. Controls over white spruce regeneration are of particular interest due to the episodic nature of seed production and problems associated with the timing of harvesting activities to coincide with the occurrence of a seed crop. Several sequential events must occur for seedlings to become established. These factors and processes control the success or failure of seedling establishment. For instance, all other factors removed, seed must be produced and dispersed onto the landscape for there to be any chance of successful seedling establishment. Furthermore, if seed is produced and dispersed, the seed must fall on a receptive seedbed in order to germinate and survive.

Seed Production

The production of white spruce cones is episodic and unpredictable (Fraser 1958, Fowells 1965, Waldron 1965, Zasada and Viereck 1970, Zasada 1971, 1972, 1980, 1985, 1986, 1995, Eis and Inkster 1972, Dobbs 1972, Safford 1974, Konishi

1985, Zasada et al. 1992, Youngblood and Max 1992, Coates et al. 1994). In the Fairbanks area of interior Alaska (Figure 4), good to excellent seed crops occur up to 12 years apart and a full 28 years separate the exceptionally large crops of 1958 and 1987 (Zasada and Viereck 1970, Zasada et al. 1992, Zasada 1995).

Rupp et. al. (1997) investigated the apparent synchrony between white spruce reproduction and climatic and tree physiological factors, identifying several "critical gateways" that must be passed for a cone crop to be realized (Figure 5-5).

Observations from the literature suggest the influence of a warm and dry growing season the year prior to seed dispersal in initiating cone crops (Lutz 1956, Matthews 1963, Zasada and Gregory 1969, Zasada 1971, Viereck 1973, Alden 1985, Zasada et al. 1992, Coates et al. 1994). Frost during flowering and rain during the pollination period may also affect the overall success of a seed crop (Zasada 1971, Farmer 1997). Several studies have identified statistically significant relationships between cone production and meteorological factors for other species (Eis 1973, Lowry 1966, van Vredenburch and la Bastide 1969).

Rupp et. al. (1997) found a positive correlation between high white spruce seed production years and the number of summer days above 26.1^{0} C in the year of bud initiation. A correlation of seed production with high fire years was also identified, suggesting synchrony of white spruce cone and seed production to environmental factors (i.e. hot and dry climate) that increases the probability of seed being dispersed onto a receptive seedbed (i.e. newly burned seedbed). Figure 5-6 shows the

relationship of high seed production years (Rupp et al. 1997) in the Fairbanks area of interior Alaska with the level of fire activity (Yarie unpublished data) in Alaska. The total area burned the year prior to seed dispersal represents a highly receptive seedbed for the germination and survival of white spruce seed dispersed upon the landscape the following year. In other words, the reproductive response of white spruce to the environment results in high production events being initiated at the same time and under the same climatic conditions that tend to produce large fire years and associated receptive seedbeds. Seed production in the Fairbanks region of interior Alaska and total area burned in Alaska the previous year had a correlation value of 0.62 for the period 1957-1976. The was no correlation (-.05) for the period 1977-1995. This suggests that environmental changes in climate may have disrupted the synchrony exhibited from 1957-1976.

A physiological response produced by the previous year's cone crop has been shown to affect the number of available sites for differentiation of reproductive buds, therefore excellent years are commonly followed by poor years (Matthews 1963, Zasada et al. 1992, Farmer 1997). Rupp et. al. (1997) found a response of decreased radial growth of trees in years of successful cone and seed production. Investigation of the relationship between cone and wood production for other species have also shown a decrease in ring width during years of cone production (Daubenmire 1960, Eis et al. 1965). Such a relationship suggests a tradeoff between reproductive and vegetative growth, resulting in reduced radial growth. The years following high seed production

are utilized to replenish growth reserves, indicated by a reduction in reproductive bud differentiation and subsequent poor seed production.

Seed Dispersal and the Seedbed

White spruce seed is dispersed primarily by wind. In interior Alaska, the majority of seed is dispersed in September and October before permanent snow cover (Zasada and Viereck 1970, Zasada et al. 1978, Youngblood and Max 1992). Several studies have investigated white spruce seed dispersal into clearcuts (Rowe 1955, Schlesinger 1970, Dobbs 1976, Zasada and Lovig 1983, Zasada 1985, Youngblood and Max 1992, Greene and Johnson 1995). Dispersal of seed from an area source can be described by a negative exponential model (Okubo and Levin 1989, Willson 1992, Farmer 1997). The density of seed is spatially variable, decreasing sharply as distance from the seed source increases (Figure 5-7). White spruce has a limited dispersal range, with few seeds being dispersed beyond 200 to 300 m from the source edge (Zasada and Gregory 1969, Dobbs 1976, Zasada and Lovig 1983, Zasada 1985, Youngblood and Max 1992). Greene and Johnson (1995) observed seed dispersal in Canada up to 475 m from the seed source and modeled potential long distance (i.e. > 300 m) wind dispersal of seed across the landscape. The effects of prevailing winds upon the seed shadow are inconclusive (Harris 1967, Schlesinger 1970, Zasada and Lovig 1983, Youngblood and Max 1992, Greene and Johnson 1995, 1996). A relationship was observed between seed dispersal, fall winds, and the seed shadow for

an upland white spruce stand in interior Alaska (Figure 5-8). Data indicate that 83.6 percent of total seed collected in the fall originated from 4 transects on the leeward side of the seed source.

White spruce seedling establishment success hinges upon the availability of a receptive seedbed. In general white spruce require a mineral soil seedbed for successful germination, survival, and seedling growth (Zasada and Gregory 1969, Zasada 1971,1972,1986, Zasada et al. 1992). Such seedbed conditions are associated with the effects of fire on the forest floor (Viereck and Dyrness 1979, Viereck et al. 1979, Viereck 1982, Dyrness and Norum 1983, Viereck and Foote 1985, Dyrness et al. 1986, Dyrness et al. 1989). Post-fire increases in soil pH, nutrient availability, microbial populations and associated nutrient cycling, depth to permafrost, light, and soil temperature all provide a favorable but highly variable environment for seedling establishment and growth. The post-fire forest floor substrate interacts with these favorable conditions to influence establishment patterns upon the landscape.

The effects of fire on the vegetative structure of the forest floor, specifically forest floor thickness, survival of competing species (i.e. Calamogrostis canadensis), competitive ability of surviving white spruce, and the soil reproductive bank potential of competing species, directly affects the establishment potential of seedlings originating from seed (Zasada et al. 1983, Fox et al. 1984, Thomas and Wein 1985, Putnam and Zasada 1986, Walker et al. 1986, Zasada et al. 1987).

Fire in interior Alaska, as well as in most fire-dominated systems, is heterogeneous in nature; producing a spatially variable pattern in both areal extent and intensity/severity effects (Lutz 1956, Quirk and Sykes 1971, Viereck 1973, Heinselman 1981, Thomas and Wein 1985, Hobbs and Atkins 1988, Ratz 1995). Furthermore, the effect of fire, within the context of the relationship between intensity/severity and post-fire vegetation structure, is spatially variable at multiple scales (Dyrness and Norum 1983, Zasada et al. 1983, Eberhart and Woodward 1987, Baker 1993). Therefore, establishment potential can be viewed from the point of initial post-fire seedbed conditions upon the landscape and the declining receptivity with time.

The use of a seed to seedling ratio, which determines the number of seeds needed to produce a seedling of a given age, can provide a general measure of the success of seedling establishment (Zasada et al. 1992). Seed to seedling ratios can be used to develop a dynamic seed:seedling index. The index represents the number of seeds needed to produce an established seedling, defined as a 5 yr free to grow seedling, and is a function of immediate post-disturbance seedbed conditions and time since disturbance. Table 5-1 shows a seed:seedling index for both southerly and northerly aspect upland white spruce. Variables such as forest floor thickness, soil pH, soil temperature and moisture, competitive species survival, and nutrient availability are implicitly represented by the characterization of the seedbed. The influence of vegetative competition for light, moisture, nutrients, and growing space is implicitly represented by time since the disturbance event.

Implications for Forest Management

Currently forest management practices for white spruce systems in interior Alaska relies upon planting activities to regenerate a harvested site. Reliance upon costly planting is the result of the inability to predict seed availability and natural seedling establishment. Zasada (1995) suggests that if land managers could better predict the production and dispersal of seed they would be more confident in using natural regeneration as a part of white spruce management. Natural regeneration would decrease costs associated with restocking as well as add genetic diversity to the system.

Predicting Seed Production

The ability to predict future white spruce crops beyond one year is questionable. Eis (1967) and Eis and Inkster (1972) describe how predictions of cone crops can be made the September preceding the seed year. Such information can be utilized for planning seedbed preparation and regeneration activities associated with a scheduled harvest. However, one cannot accurately predict future cone crops beyond one year. That information could be used for the advance planning of harvesting activities.

The "critical gateways" conceptual model offers additional information and insight for the land manager (Figure 5-5). For instance, if the current seed crop is large, the likelihood of a seed crop the following year is near zero, due to growth

reserve limitations. If the current summer temperatures are high and the current seed crop is not significant the probability of a seed crop the following year increases. Although such information does not provide definitive answers it does increase the land manager's knowledge base and provides information that can increase the probability of a successful natural regeneration program.

The Seed Shadow

Information on the dispersal of seed from a source coupled with seed production information provides the necessary information to describe the distribution of seed upon the landscape. Figures 5-7 and 5-8 provide some general information on the dispersal of white spruce seed in interior Alaska. Maximizing the seed shadow of a source increases the probability for natural regeneration. Proper seed source orientation, relative to wind direction, could increase both the density and areal extent of seed upon the landscape.

An effective distance threshold could be used to represent the maximum distance at which an acceptable level of seedlings would become established. This threshold would change with both changing seed production levels and changing seedbed conditions. For instance, given a certain production level, the effective dispersal distance would be greater on a more receptive seedbed. In other words, the more receptive the seedbed (i.e. mineral soil vs. 8 cm organic layer) the less seed

needed to produce an established seedling. The same would hold true for increased production levels. Given the same seedbed receptivity, as seed production levels increase so does the effective dispersal distance.

Site Preparation and Planting

Information on seedbed conditions and the receptivity of a particular seedbed to white spruce seed can provide the land manager with important site preparation information. The use of a seed:seedling index (Table 5-1) coupled with information on seed production and dispersal information allows one to concentrate site preparation and planting activities to areas that will not regenerate naturally. Such information could be used to provide site preparation to areas that under optimal conditions would receive enough seed to naturally regenerate the site. In other words, one could maximize the effective dispersal distance. Areas beyond this effective distance threshold could be planted to assure adequate restocking levels.

Simulating the Early Establishment Pattern of White Spruce Seedlings

The ability to simulate potential establishment patterns of white spruce on the landscape would be a useful forest management tool. A spatially explicit model of early regeneration dynamics for interior Alaska, the Alaskan Boreal Forest

Establishment Model (ABFEM) has been developed. The model simulates the production of seed, dispersal of seed, disturbance effects upon the seedbed, vegetative reproduction potential, and early establishment patterns of white spruce, paper birch, and aspen seedlings upon the landscape (see Chapter 4). ABFEM provides geographically explicit information that can assist the land manager in management decisions and aide in the development of harvest layouts. The model provides output of potential use for several management issues including: identifying areas that may not regenerate naturally, maximizing the area of potential natural regeneration success, and identifying areas needing specific site preparation and/or seedling planting activities.

Natural Recolonization Potential

Simulating the natural recolonization patterns of forest tree species upon a disturbed landscape provides the ability to investigate potential establishment scenarios and the resulting early establishment patterns upon the landscape. This information can be of particular interest for white spruce, with episodic seed production that can have a profound influence upon post-disturbance recolonization patterns. Figure 5-9 shows a 6 year predicted recolonization pattern of white spruce within a large burned area outside the Fairbanks area of interior Alaska. Such information can provide the land manager with a measure of the potential natural regeneration success of an area. Simulations of "worst case" scenarios, for example little or no seed production for 10

years following a disturbance, can provide information to the land manager to assist in the management action decision making process.

Forest Management

Simulating natural regeneration patterns following harvesting can assist in harvest layout and silvicultural planning. The forest manager can use the model as a virtual laboratory where the results of a silvicultural plan can be investigated. The manager can simulate various scenarios and utilize the results to aide in silvicultural planning. ABFEM was used to simulate natural seedling densities, following three different harvesting schemes.

Three harvest schemes, a clearcut, strip cut, and residual tree islands, were simulated on the same "generic" landscape (Figure 5-10). Each scheme differed in the type of regeneration cut implemented, however the total residual stand area (8 hectares) was the same for each simulation. Each simulation was run for an excellent (200,000 viable seeds / 100 m^2), good (80,000 viable seeds / 100 m^2), and a moderate (30,000 viable seeds / 100 m^2) production event. All input and parameters, including random seedbed conditions, were kept constant for each simulation.

A comparison among the model experiments revealed distance from the seed source as a major limitation to natural regeneration across the landscape. Distance from the seed source was a major limiting factor to seedling establishment in the clearcut experiment. For all three production levels the clearcut landscape had several

hectares with no seedlings. There were 3.2, 5.0, and 6.0 hectares without seedlings for the excellent, good, and moderate production events, respectively.

Figure 5-11 shows significant difference in seedling density between the clearcut and both the strip cut and residual islands. The average number of seedlings per 100 m^2 was low (i.e. < 16 seedlings per 100 m^2 , a stocked stand) for all moderate production events, regardless of harvest method. In other words, at moderate production levels, seed availability is the limiting factor for seedling establishment success. Furthermore, the clearcut method resulted in low average density regardless of the production level, indicating a dispersal distance limitation.

Further comparison among the model experiments can be made regarding the stocking "efficiency" of an individual harvesting layout. By calculating the ratio of stocked (i.e. $\geq$ 1600 seedlings/ha) to understocked area, we can compare the relative ability of a particular regeneration cut in attaining adequate stocking levels within the harvested area. Figure 5-12 reveals high numbers of understocked cells (10 m x 10 m), for all moderate production events and for all clearcut scenarios.

The stocking "efficiency" of the different model scenarios shows significant variability among harvest methods and among production levels (Figure 5-13). Only the strip-cut and residual islands, under a non-moderate production event, succeeded in restocking 50 percent or more of the harvested landscape. The very high stocking "efficiency" for the strip-cut and residual islands, under an excellent production event,

suggests the harvested area could be expanded and still allow for adequate restocking by the residual stand.

It should be noted that their are many other silvicultural strategies utilized throughout the boreal forest. The examples presented here are meant only to provide some insight into the potential use of the model as a management tool. Systems such as shelterwoods need to be viewed differently than the current model version. Currently, the model views seed sources as points of dispersal where seed is dispersed across the landscape. Modeling shelterwood systems would involve changing the method in which the model views dispersal. A shelterwood could be modeled by altering the seed production routine and doing away with seed dispersal (i.e. we would produce and disperse the seed within the source stand). Such simulations would provide valuable information to the potential restocking of a disturbed stand or landscape.

Summary

Natural regeneration is an important component of forest management and sustainability. Understanding controls upon seedling establishment is important information for the land manager. An improved knowledge of controls upon white spruce regeneration in interior Alaska is critical to successful sustainable management of white spruce upon the landscape. Model simulation of the potential early establishment patterns of seedlings from seed provides a useful forest management tool.

Critical controls upon successful white spruce seedling establishment in interior Alaska includes the production and dispersal of seed upon the landscape and the receptivity of the seedbed. The episodic nature of white spruce seed production and its limited dispersal capabilities make it extremely difficult to predict the availability of seed across the landscape. The life history traits of white spruce reflect a synchrony to the environment and its response to the overriding influence of fire on the structure and function of the boreal forest landscape. The specific mineral soil seedbed requirements of white spruce support this synchronous response to the environment and disturbance regime. The relative short window of seedbed receptivity following disturbance coupled to its episodic seed production trends result in further complexities and difficulties in managing for white spruce natural regeneration.

Understanding the controls upon white spruce seedling establishment patterns can improve the land manager's confidence and ability to implement and utilize white spruce natural regeneration. Information regarding factors that control seed production coupled with information on the dispersal of seed onto the landscape provide an improved understanding of the availability of seed upon the landscape (i.e. the seed rain). Knowledge of seedbed receptivity provides a measure of the potential for establishment of seedlings across the landscape. Integrating seed rain information with a seed:seedling index, which indicates the establishment potential of a specific seedbed, provides the land manager with the ability to portray potential establishment patterns.

Model simulations identified both distance from the seed source and seed production as major limitations to successful restocking of a harvested site. These simple experiments suggest that large clearcuts are not an efficient harvesting strategy for promoting natural regeneration success across the landscape. Furthermore, poor seed production events provide little opportunity for the establishment of a new white spruce cohort. These results suggest that harvesting a stand during a period of poor seed production will require seedling planting if adequate restocking levels are desired.

Simulation modeling, such as that described with ABFEM, allows investigation of the resultant seedling establishment pattern on the landscape, given a specific set of environmental conditions. The model serves as a landscape laboratory, where the land manager can simulate various harvesting and silvicultural plans and view the potential response of the system. This provides a powerful tool to investigate the response of white spruce systems, in terms of seedling establishment patterns, to different disturbance scenarios.

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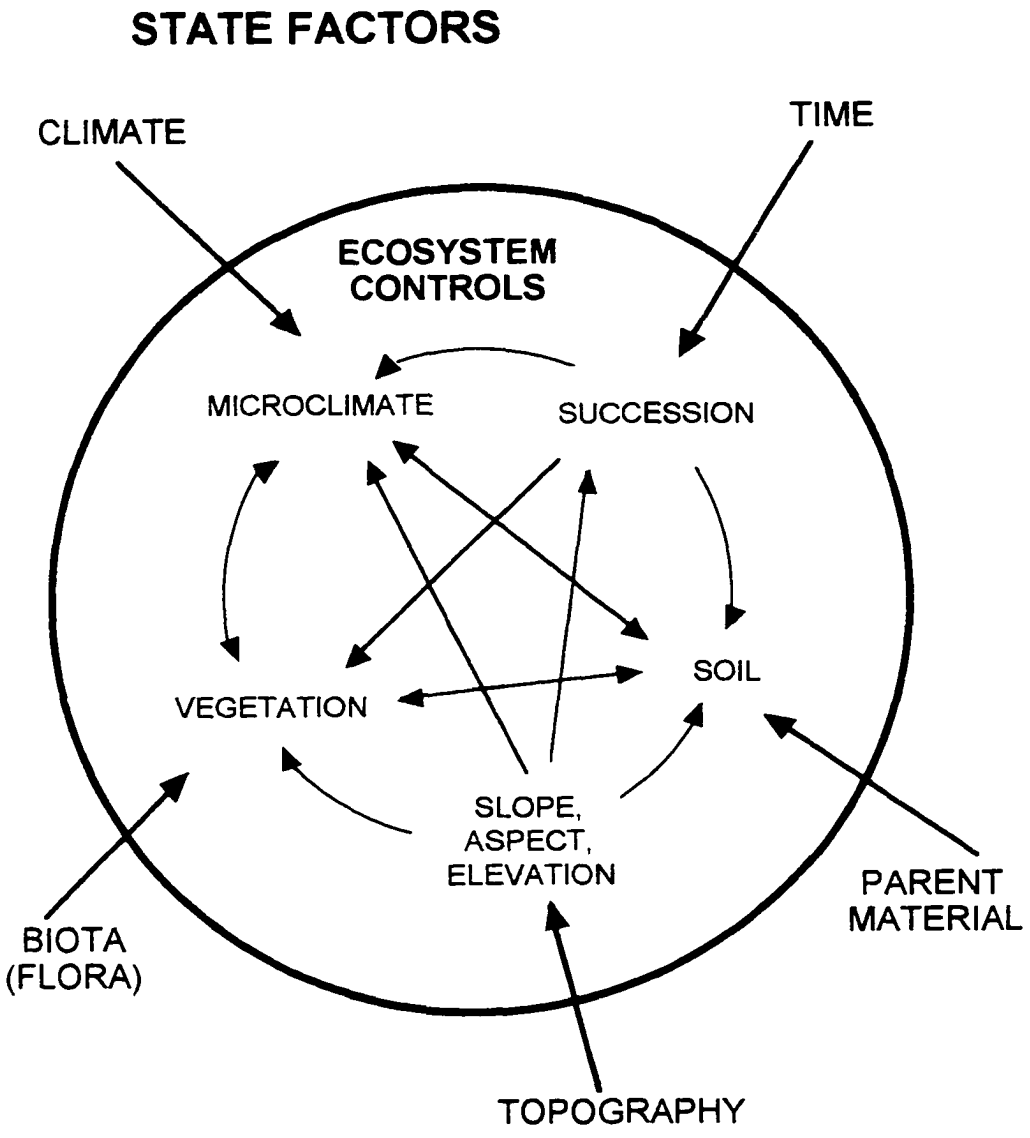

Figure 5-1. Conceptual diagram of state-factors and ecosystem controls that determine vegetation trajectory (adapted from Van Cleve et. al. 1991).

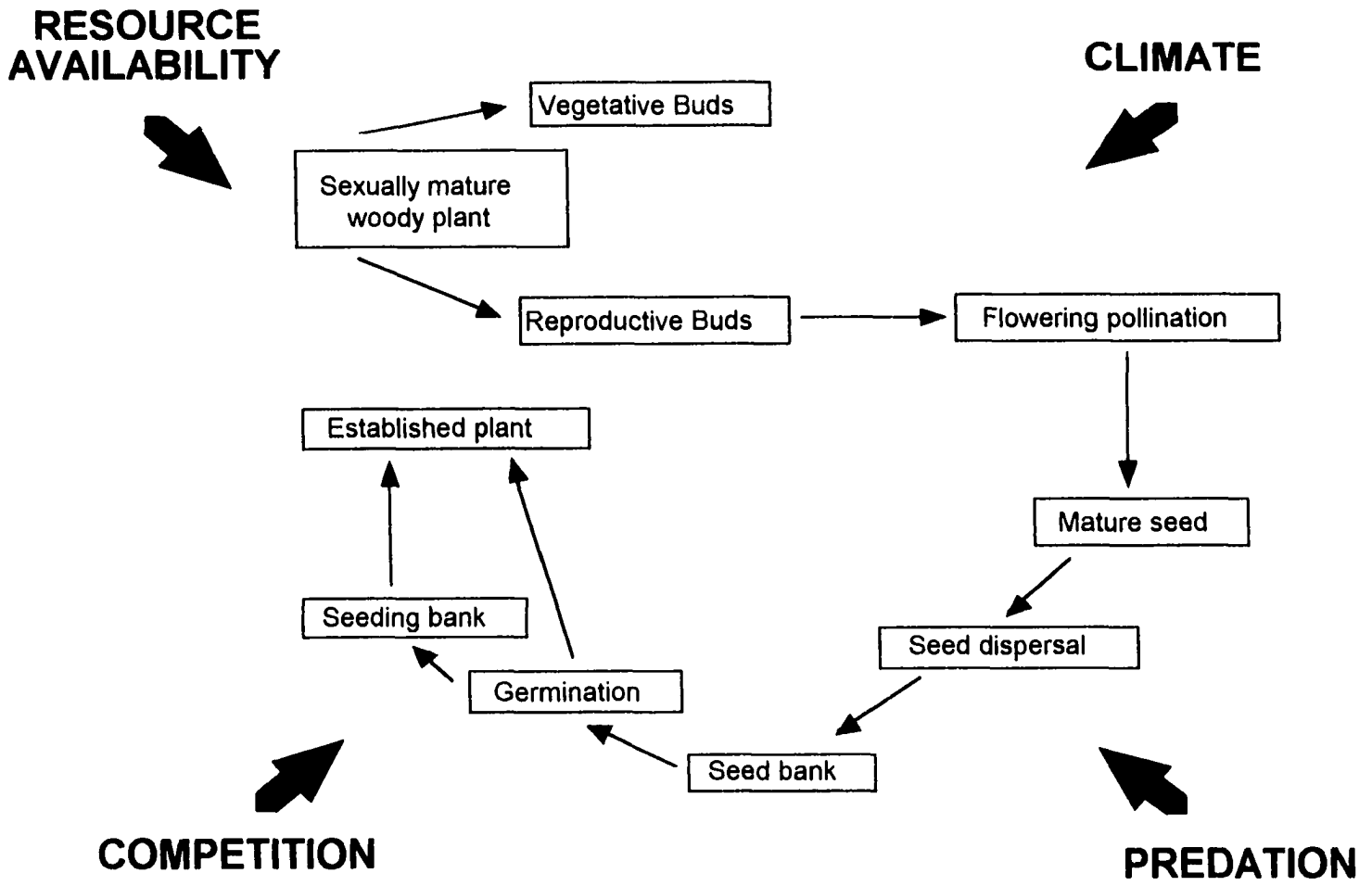

Figure 5-2. Conceptual diagram of forest tree seed reproduction cycle and important controls on seed production frequency, quality, and quantity (adapted from Zasada et. al. 1992).

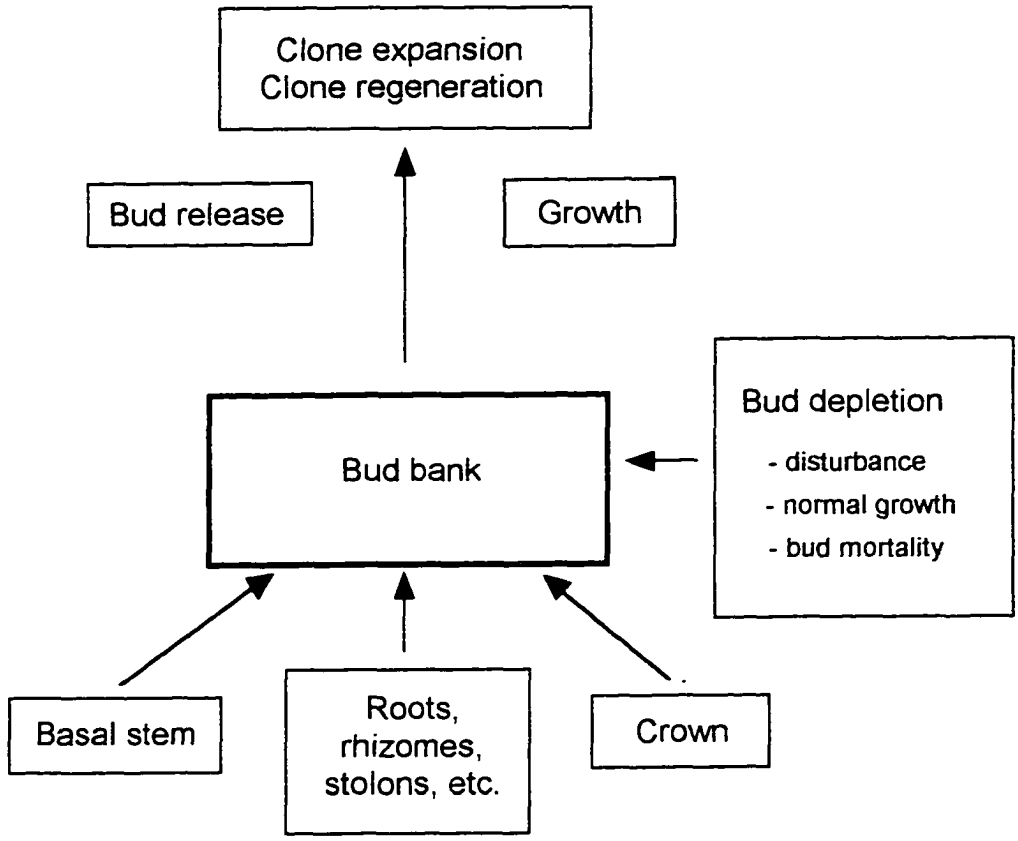

Figure 5-3. Conceptual diagram of boreal forest vegetative reproduction cycle and important controls on bud bank vigor (adapted from Zasada et. al. 1992).

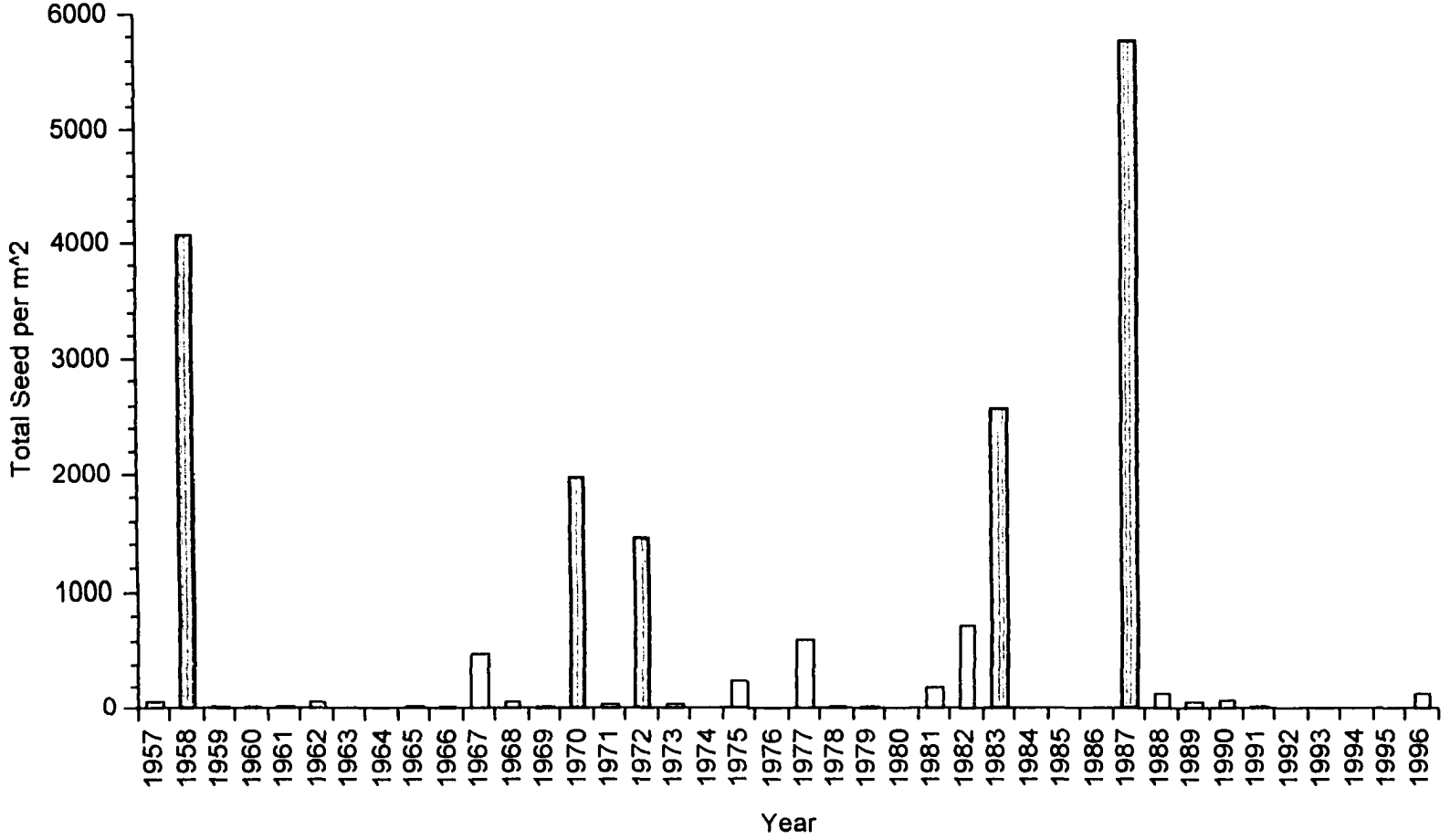

Figure 5-4. White spruce average annual within stand seed production trends from the Bonanza Creek Experimental Forest (BCEF) for the period 1957 to 1996 (Rupp et. al. 1997). Shaded bars represent exceptional production years. Average seedfall was calculated from two sites (n = 2) within BCEF.

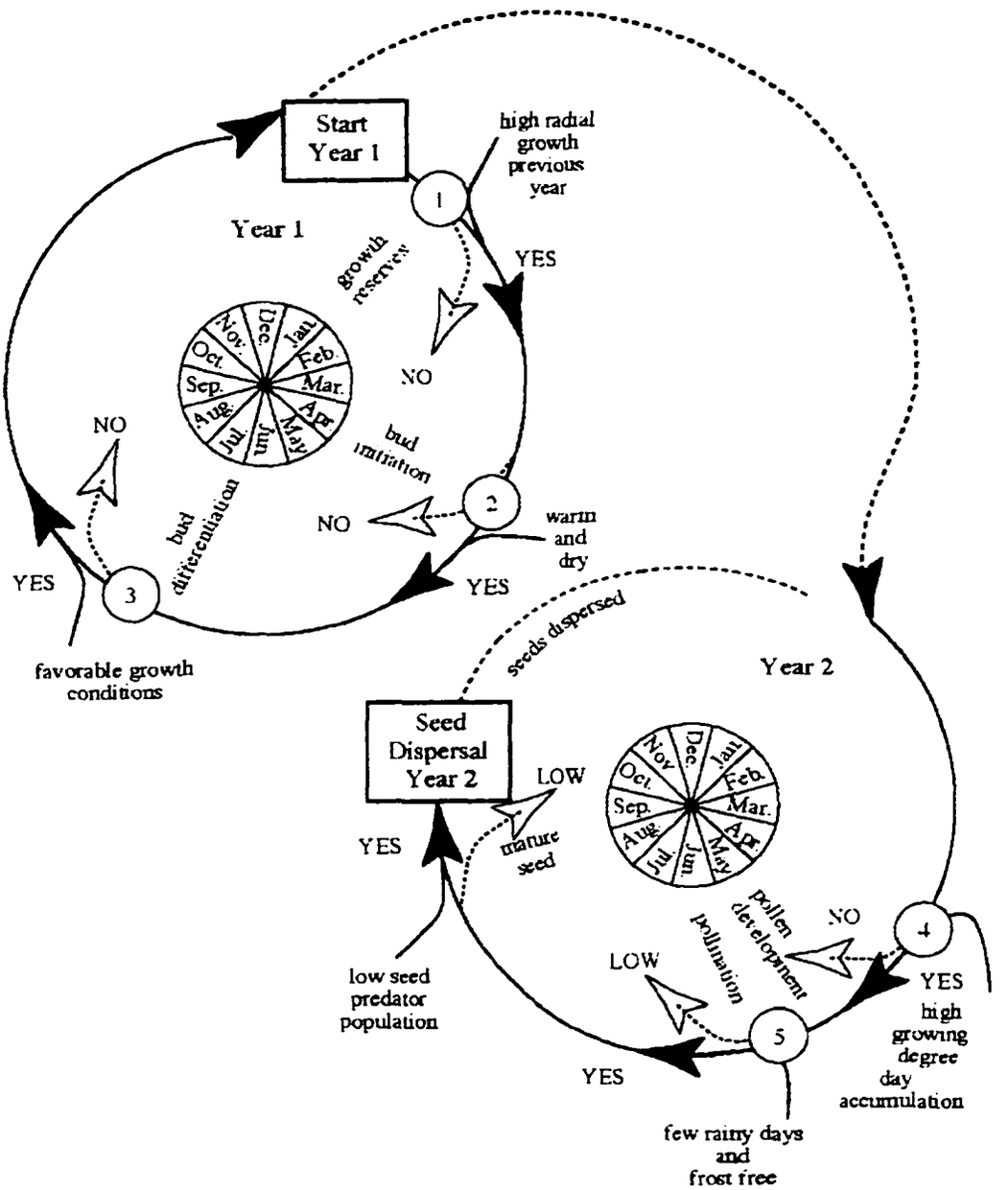

Figure 5-5. White spruce seed production critical "gateways" conceptual model (Rupp et. al. 1997). Gateways represent important controls that determine the frequency, quality, and quantity of seed produced annually.

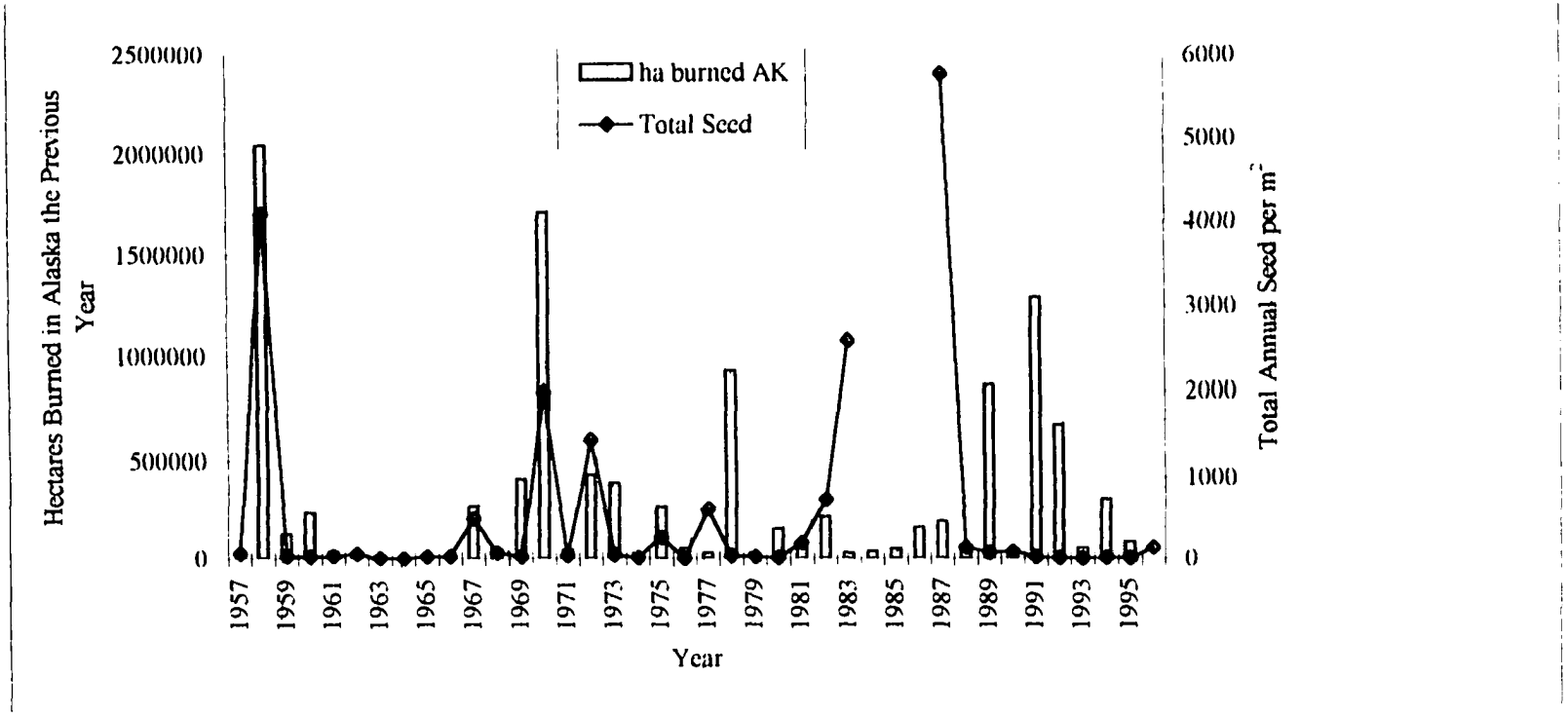

Figure 5-6. Comparison of white spruce seed production events (Rupp et. al. 1997) and total annual hectares burned in Alaska (Yarie unpublished data) the previous year. The legend is: production events (gray bars) and total annual ha burned (—). The total area burned represents a "window" of seedbed receptivity. Bud initiation of the observed crops occurred the previous summer (i.e. the year of fires). Correlation 0.62 for the period 1957-1976. No correlation (-0.05) for period 1977-1996.

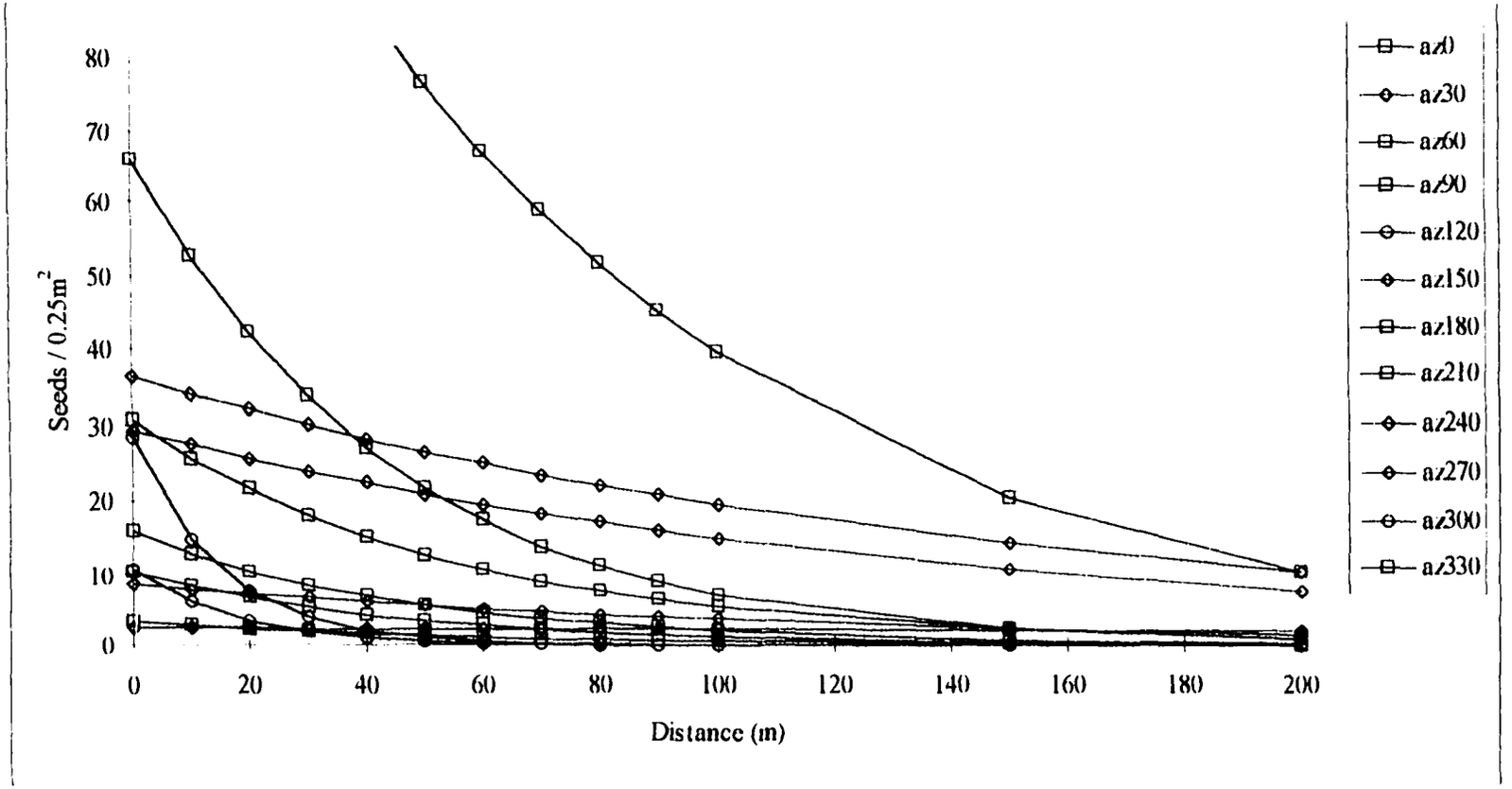

Figure 5-7. White spruce 1996 seed dispersal regression curves for individual transects at the Bonanza Creek Experimental Forest (BCEF) site. Regression line colors represent curves with similar slope. The seed trap sample size for each transect was 14 (n = 14).

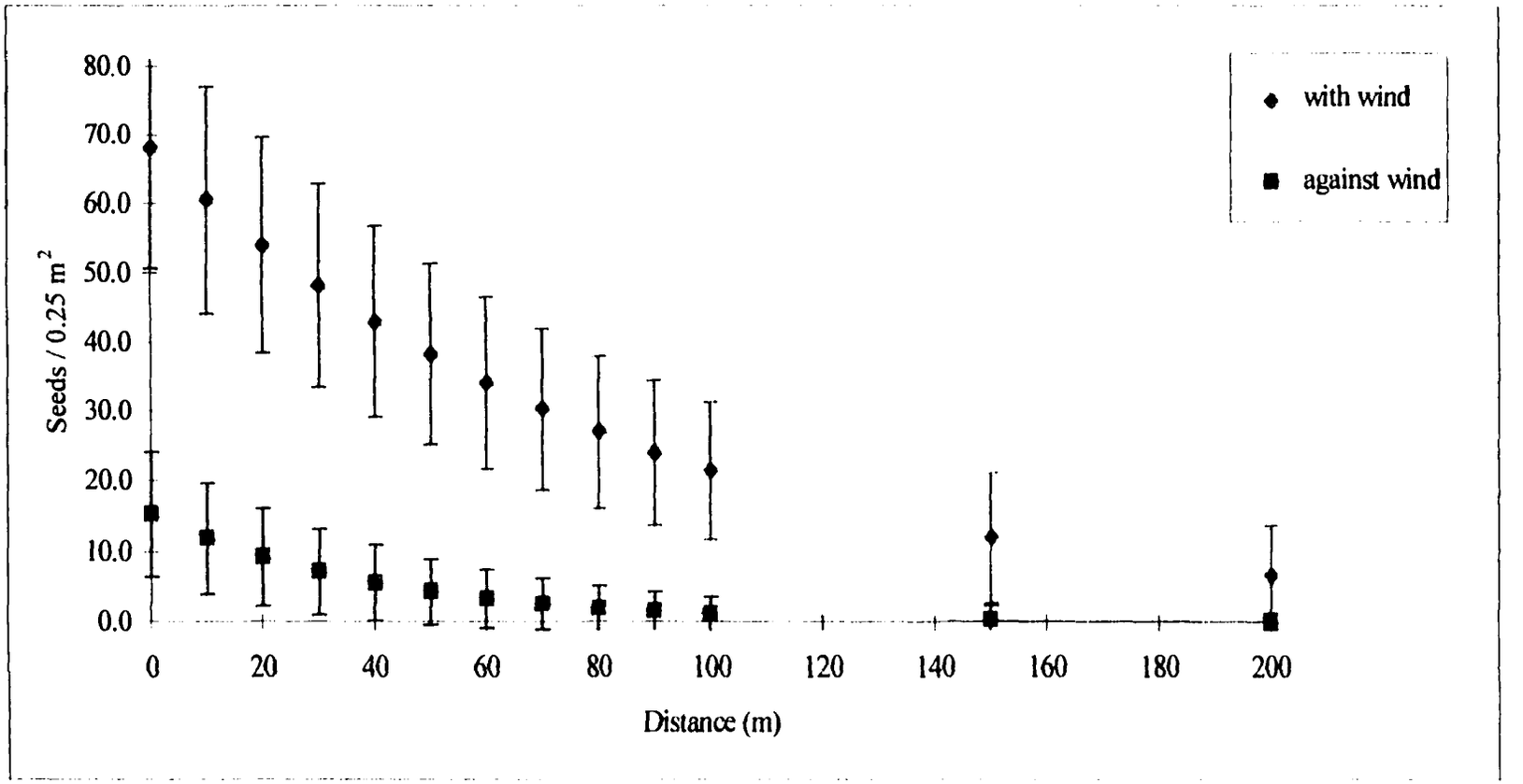

Figure 5-8. Comparison of leeward and windward white spruce seed dispersal transects at the Bonanza Creek (BCEF) site. The green line represents the leeward transects (AZ 180, 210, 240, 270) and the red line represents the windward transects (AZ 0, 30, 60, 90, 120, 150, 300, 330). Error bars represent a 95 percent confidence interval for the asymptotic standard error of the slope coefficient (b_1).

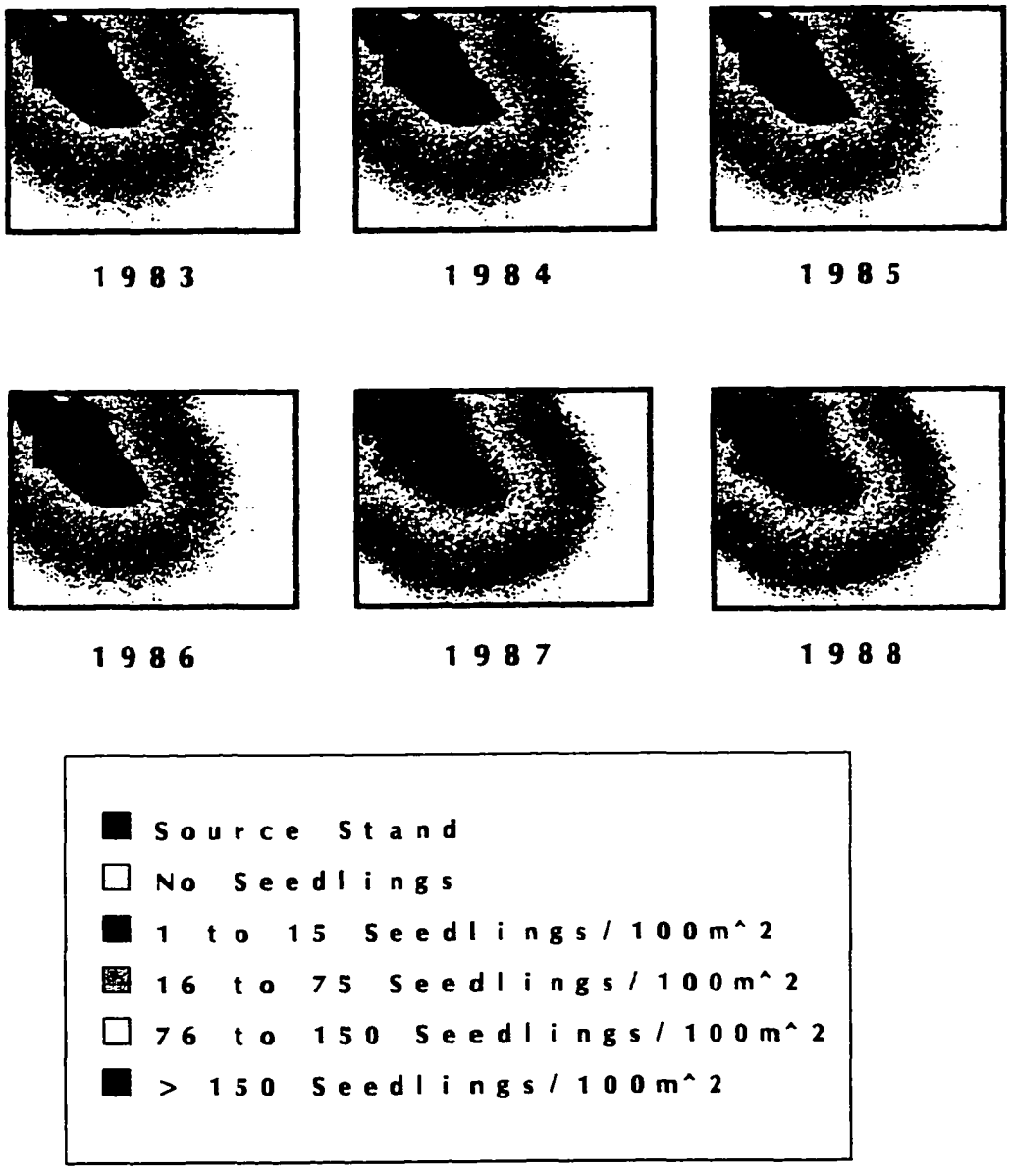

Figure 5-9. Composite map of predicted natural seedling regeneration pattern for a 6 yr simulated period (1983-1988) at Bonanza Creek (BCEF).

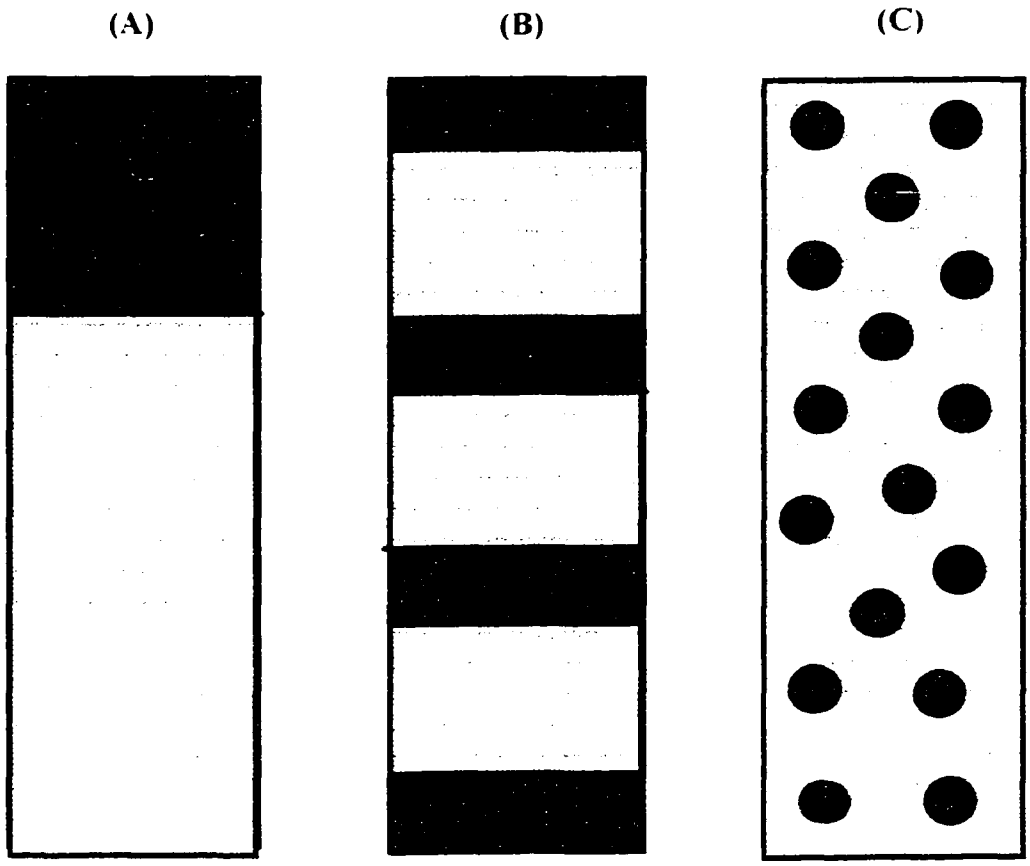

Figure 5-10. Harvest scheme for silvicultural experiments. (a) Clearcut [12 ha], (b) strip-cut [100 m wide], and (c) residual tree islands [.5 ha]. Each landscape retained 8 hectares of residual trees, harvesting removed 12 hectares.

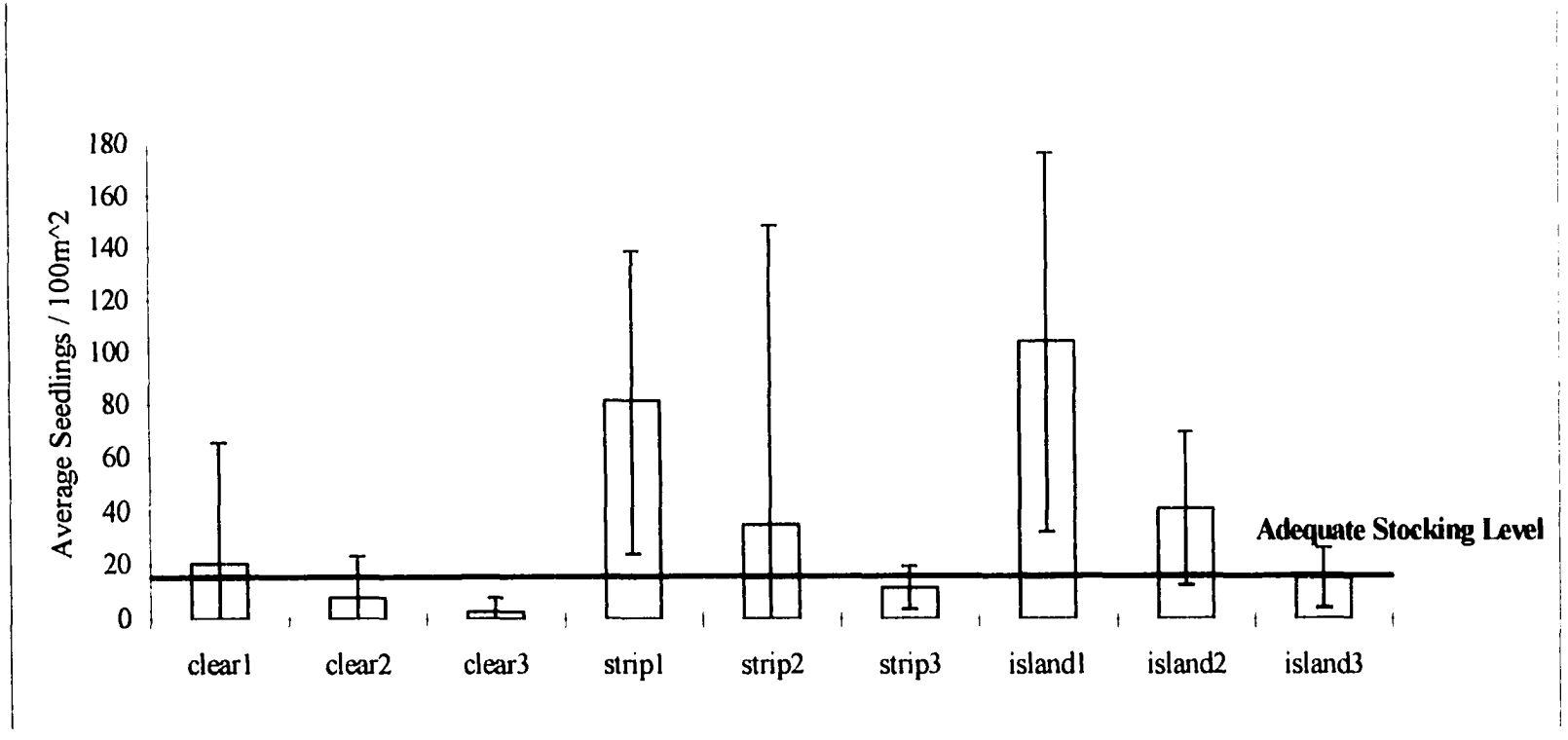

Figure 5-11. Average white spruce seedling density of the harvested landscape (12 ha) for a clearcut, strip-cut, and residual tree islands harvesting experiments, 1 yr following disturbance. Residual stand area was the same (8 ha) under each scenario. The seedbed was heterogeneous (i.e. random) Adequate stocking level represents 1553 seedlings/ha. Error bars represent a 95 percent confidence interval .

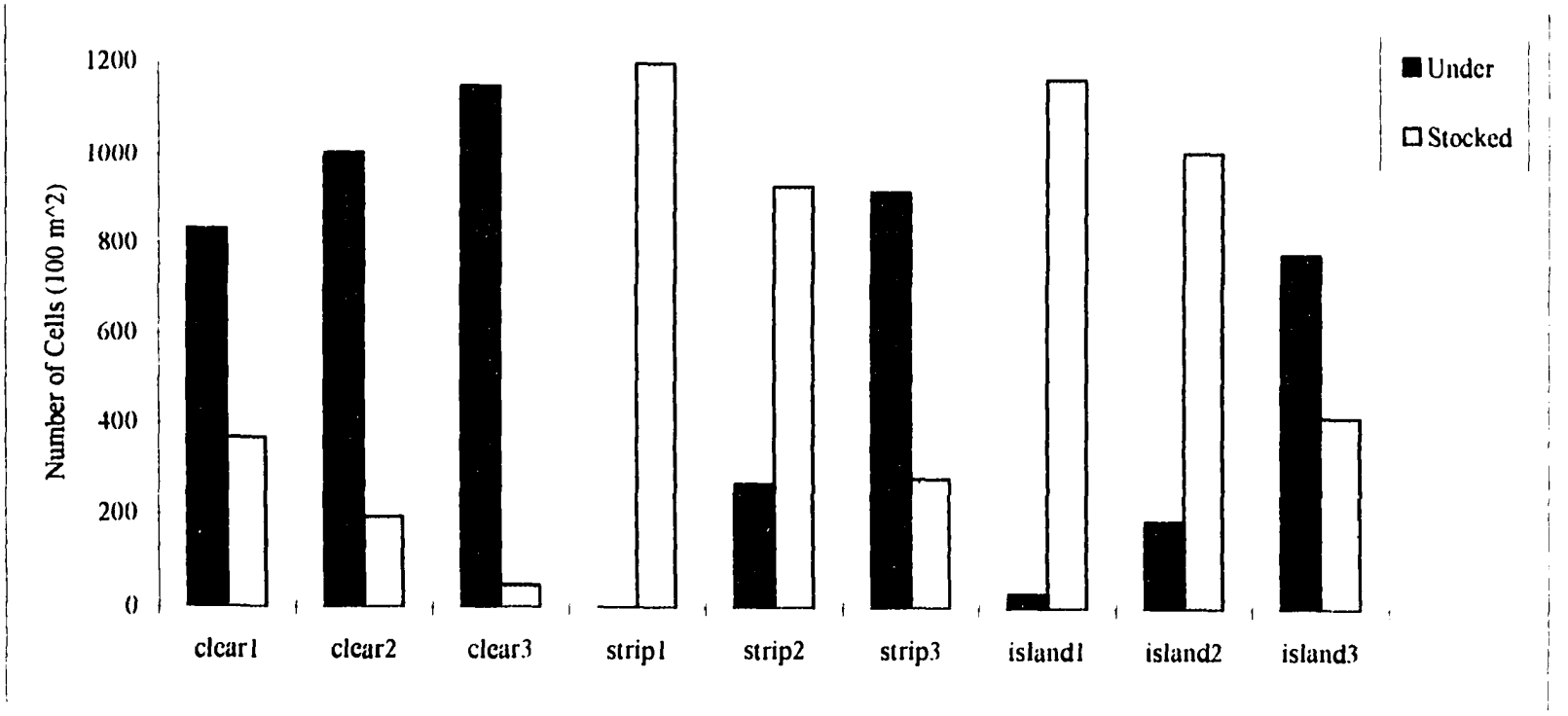

Figure 5-12. Number of stocked and understocked grid cells (100 m^2) under a clearcut, strip-cut, and residual tree islands harvest scenarios. Total area harvested was 12 hectares.

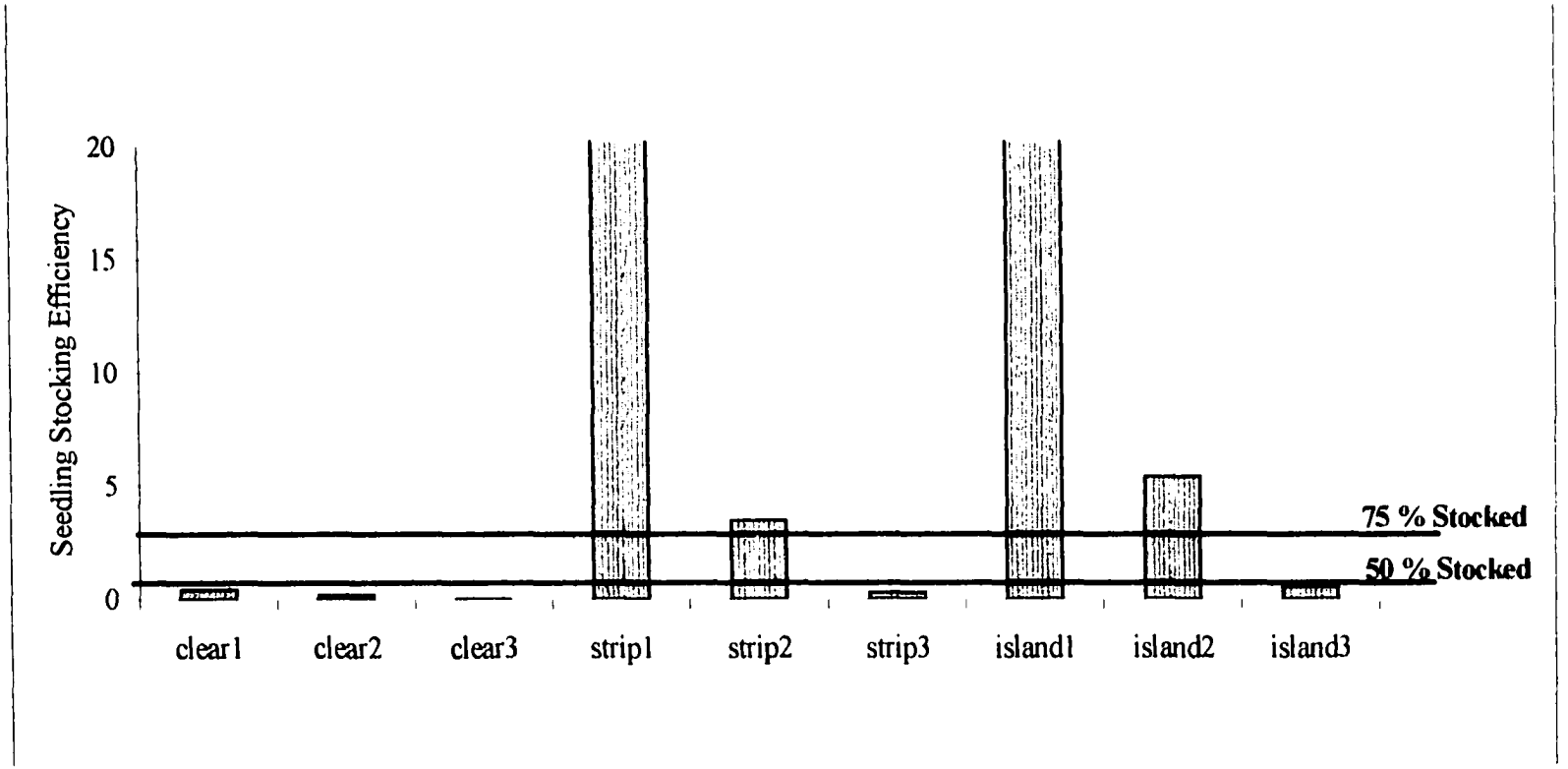

Figure 5-13. Stocking efficiency for the clearcut, strip-cut, and residual tree islands harvesting scenarios. Stocking efficiency is the ratio of stocked (1553 seedlings/ha) to under-stocked (< 1553 seedlings/ha) area. Stocking efficiency provides a measure of natural regeneration strength. The 50 and 75 percent stocking thresholds represent a harvested landscape that is 50 and 75 percent, respectively, stocked in total area.

Table 5-1. Dynamic seed:seedling index for white spruce on (a) northerly aspects and (b) southerly aspects. Showing the average number of viable white spruce seed needed to produce one 5 yr old free to grow seedling on a given seedbed substrate and at a given time since initial disturbance.

(a)

	Initial Burn Severity				
Time[1]	Unburned	Scorched	Light	Medium	Heavy
1 Yr	2200	2000	1400	500	100
2 Yr	2200	2200	1600	1000	250
3 Yr	2200	2200	1800	1600	500
4 Yr	2200	2200	2000	1800	1000
5+ Yr	2200	2200	2200	2000	1600

(b)

	Initial Burn Severity				
Time[1]	Unburned	Scorched	Light	Medium	Heavy
1 Yr	2500	2300	1500	750	500
2 Yr	2500	2500	1900	1500	1000
3 Yr	2500	2500	2100	1900	1300
4 Yr	2500	2500	2300	2100	1700
5+ Yr	2500	2500	2500	2300	1900

[1] indicates time since disturbance

CHAPTER 6 - CONCLUSIONS AND RECOMMENDATIONS

This study of upland white spruce ecosystems in interior Alaska was conducted to identify important controls over early forest establishment dynamics following disturbance and develop a spatially explicit model of seedling establishment patterns on the landscape. The specific study objectives were: (i) identify important environmental factors and ecological processes influencing early seedling establishment, (ii) develop a theoretical model to represent early regeneration dynamics within the framework of a geographic information system GIS, (iii) develop a spatially explicit model of early post-disturbance seedling establishment patterns for upland white spruce ecosystems, and (iv) validate the model with existing information on white spruce seed production, seed dispersal, and seedling establishment patterns.

Post-disturbance regeneration dynamics of upland white spruce systems are complex. Establishment patterns are a function of the interacting variables of seed availability and seedbed receptivity. The availability of seed is a function of three major variables: (i) the proximity of a seed source, (ii) the production of seed, and (iii) the dispersal of seed upon the landscape. Seedbed receptivity is a function of two variables: (i) the immediate post-disturbance seedbed characteristics and (ii) the increasing site occupation by competing vegetation as time since disturbance increases.

Successful white spruce seedling establishment requires the timing of available seed at a sufficient density encountering a receptive seedbed to produce a cohort of

established seedlings upon the landscape. The greater the amount of available seed the greater the probability of successful seedling establishment. Likewise the greater the receptivity of the seedbed the greater the probability of seedling establishment success.

The overriding control upon seed availability is the episodic nature of white spruce seed production. That seed is produced infrequently and irregularly, decreases the probability that seed will be available concurrently with a receptive seedbed. The presence of a nearby seed source and the maximum seed distance limit the distribution of seed across the landscape.

The receptivity of a seedbed, in terms of providing favorable conditions for a seed to germinate, survive, and grow is initially controlled by the effects of disturbance on the structure and function of the seedbed. After which it is dominated by the increasing occupation of the site by other species. Immediate disturbance effects upon both the overstory and forest floor dictate the amount and intensity of competition for the seedbed's site resources of light, moisture, nutrients, and growing space. In general the severity of disturbance is positively correlated to the receptivity of the seedbed, both immediately following the disturbance and with the progression of time since disturbance. Increasing occupation of a site by competing species results in a relatively short window, in terms of seedbed receptivity, for successful colonization and establishment success of a site.

The ability to simulate the potential early post-disturbance establishment pattern of seedlings in an upland white spruce ecosystem on a defined landscape provides a

tool for forest management. A spatially explicit model allows the realistic description of landscape regeneration dynamics and identifies the importance of pattern and neighborhoods on seedling establishment. The spatially explicit nature of the model lends itself for use in the decision making process of forest management. Specifically, the model can provide the following information important to forest management issues: (i) simulation of the potential recolonization patterns of a disturbed landscape, (ii) simulation of the potential effects of seed source orientation and shape upon the seed shadow and subsequent regeneration, both areal extent and density, (iii) simulation of the potential effects of site preparation upon the extent and density of seedling establishment, and (iv) the identification of areas to concentrate site preparation and planting efforts to maximize restocking of a disturbed area and minimize associated costs of restocking.

The model (ABFEM) simulates the production, dispersal, and early establishment of seedlings on the landscape. A simplistic representation provides two basic advantages. First, by minimizing the complexity of the model, ease of investigation of changes in the key driving variables (i.e. controls) and subsequent results is facilitated. Second, by representing only the most responsive processes and factors the model provides real world applicability for forest managment.

The model performed well at describing general seedling establishment pattern following fire. The predicted seedling densities correlated well with measured seedling densities at Bonanza Creek Experimental Forest. However, the model failed to

reproduce specific years and site results. Although much research has been conducted on regeneration of white spruce in interior Alaska, there is still a great amount of information needed to provide land managers with a solid knowledge base of white spruce natural regeneration dynamics.

The model identified information gaps and areas of limited information including, white spruce seed production, seed:seedling ratios of white spruce and paper birch, and vegetative regeneration of aspen and paper birch. Our knowledge of the processes of seed production and dispersal is limited with only a generalized idea of seed availability upon the landscape and its controls. Additional information on seedbed receptivity and the development of detailed seed:seedling indexes for interior Alaska tree species is warranted. Furthermore, empirical data regarding the observation of natural regeneration patterns across the landscape are lacking. More detailed information, such as seed:seedling indexes, and the existence of empirical data sets would allow further model calibration and validation. Such information would provide a better understanding of natural regeneration, particularly for interior Alaska white spruce systems, and provide increased confidence to the land manager for developing natural regeneration management practices.

Future research should be directed towards increasing the level of information, specific to natural regeneration pattern and control in interior Alaska, and collection of empirical data for testing and validation. Further model development, calibration, and validation are needed to provide an accurate model of early establishment patterns.

This includes an improved predictive seed production routine, more detailed seed:seedling indexes, and data of natural establishment patterns of white spruce ecosystems following disturbance. The opportunity to further develop the model for use as a forest management tool is great and could provide a very powerful simulation tool to aide in forest management decision making and planning.